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AMERICAN MALACOLOGICAL BULLETIN

VOLUME 16 2001 NUMBER 1/2

Journal of the American Malacological Society

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EDITORIAL COMMENT

The publication of this volume of the *American Malacological Bulletin*, 16(1/2), marks the 15th year of my association, first as managing editor (1986-93) and then Editor-in-Chief (1993 to date), with this journal publication. Over this period of time it has been my privilege to have served the American Malacological Society, and in doing so, to have worked with a large, diverse, and distinguished group of malacologists worldwide in their capacities as contributing authors, reviewers, and members of various AMS committees and councils, as well as many AMS members-at-large. As with the organisms to which we have dedicated our research interests, this journal is in its own way an evolving organism, needing to pass occasionally to new leadership who can provide renewed energies, new vitality, and new perspectives. This process is healthy. To facilitate this continued growth and development, as well as my need to refocus increments of time that continually grow more precious, I resign my editorship of the *Bulletin* with the publication of this volume.

The *Bulletin* and my efforts as Editor-in-Chief benefited continuously from the substantial contributions of many individuals over the past 15 years. Robert Prezant first asked me to serve with him as managing editor. Bob's tutelage was invaluable and much of what I know of editorial operations is a result of his informed instruction. Paula Mikkelsen and Tim Pearce served with me as managing editors during the period of time I have been Editor-in-Chief. To them, in their turn, fell the many responsibilities of copy editing, working with authors to finalize revisions, and interfacing with our printer. I appreciate their collegiality and dedication. Also, my thanks go to the members of the editorial board, composed at various times of Melbourne Carriker, George Davis, James Nybakken, Robert Prezant, W. D. Russell-Hunter, Amalie Scheltema, and Thomas Waller. Also, my special thanks go to Patricia Burbridge, my administrative assistant at UCA, who provided invaluable service.

An additional asset has been the long and beneficial relationship of this journal with Shaughnessy Printing Company in Biloxi, Mississippi, notably its owner Mr. Denny Shaughnessy. Special thanks also go to Carol Underwood who, as our typesetter, helped to ensure quality control at many stages of the publication process.

On a more personal note, the time that I have devoted to my editorial responsibilities has come, in part, as a donation of time that otherwise would have been spent with my wife, Kathy. To her go my thanks for her understanding and willingness to generously and good naturedly donate to the AMS time that I might otherwise have given to her. The same can be said for my three children, Alexandria, Micah, and Danielle, who have known of the existence of the *Bulletin*, and the time demands that it placed upon their father, for essentially their entire lives.

I originally agreed to take on the managing editorship because of what I felt was my responsibility and obligation to repay a professional society that had given me ample opportunities to present my research findings and interact with established malacologists during the period that my career was in its formative stages. While I will miss the energy and excitement of the editorship, I leave feeling that my debt is now repaid.

Over the nearly two decade history of the AMB in its current form, the *Bulletin* has grown and matured to be in a strong position to continue serving the world of malacological scholarship and the membership of the AMS. The number of submissions is higher now than ever in its history, there are more authors from more different countries contributing their manuscripts, and the topics in malacology have broadened to include new taxa descriptions as well as aspects of ecology, physiology, and phylogeny. Indeed, this volume begins with a paper on larval ornamentation in ammonoid cephalopods, and the next one will contain a paper describing a new species of rostroconch.

I leave the editorship convinced that the future of the *Bulletin* is bright and that it will continue to be a source of pride to our membership. In addition, the *Bulletin* will continue to serve as a welcoming extension of our organization to all malacologists here and abroad.

Ronald B. Toll
August 2001

Micro-ornamentation on the embryonic and postembryonic shells of Triassic ceratites (Ammonoidea)

Neil H. Landman[1], Fabrizio Bizzarini[2], Kazushige Tanabe[3], Royal H. Mapes[4], and Cyprian Kulicki[5]

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Abstract: The ceratites *Trachyceras (Trachyceras) aon* (Münster, 1834) and related species in the family Trachyceratidae from the Upper Triassic (lower Carnian) San Cassiano Formation of Italy display a tuberculate micro-ornamentation on their embryonic shells (ammonitellas). The tubercles are irregularly distributed over the exposed portions of the ammonitella and terminate at the ammonitella edge. The tubercles are approximately 4 µm in diameter and are extensions of pseudohexagonal trillings in the outer prismatic layer of the shell wall. This micro-ornamentation is similar to that on the ammonitellas of other Mesozoic ammonoids including Phylloceratina, Ammonitina, Ancyloceratina, and Lytoceratina, and different from that on the ammonitellas of Paleozoic ammonoids including Agoniatitina, Anarcestina, Tornoceratina, and Goniatitina. The presence of this tuberculate micro-ornamentation may represent a synapormorphy for Mesozoic ammonoids.

These ceratites also display a micro-ornamentation on their postembryonic shells consisting of tubercles and ridges aligned in longitudinal rows. This micro-ornamentation has been observed in several species of Jurassic ammonites and bears some resemblance to the wrinkle layer. However, unlike the wrinkle layer, it probably formed at the growing edge of the mantle and reflected the ornamentation of the periostracum.

Key Words: ammonoids, Triassic, embryonic shell, micro-ornamentation

The micro-ornamentation on the embryonic shell (ammonitella) of ammonoids has been described in several suborders including the Agoniatitina, Anarcestina, and Tornoceratina, where it consists of transverse lirae, in the Lytoceratina, Ancyloceratina, Phylloceratina, and Ammonitina, where it consists of tubercles, and in the Goniatitina in which the ammonitella is smooth (see the recent review by Landman *et al.*, 1996; for goniatites, see Kulicki *et al.*, in press,b). In this paper, we describe for the first time the micro-ornamentation on the ammonitellas of ceratites and comment on the phylogenetic implication of this finding. We also document the micro-ornamentation on the postembryonic shells of these species.

MATERIAL AND METHODS

The ceratites studied belong to *Trachyceras (Trachyceras) aon* (Münster, 1834), *T. (T.) muensteri* (Wissmann, 1841), *T. (Brotheotrachyceras) larva* (Klipstein, 1843), and related species in the family Trachyceratidae. The specimens are from the Upper Triassic (lower Carnian) San Cassiano (= St. Cassian) Formation of Prati di Stuores in the Italian Dolomites (see Figs. 1 and 2 for a map of the region and a generalized stratigraphic section, respectively). The ammonoids and other faunal elements of this formation have been extensively studied because of their superb preservation (see Urlichs, 1974, 1994; Bizzarini, 1988, 1996; Bizzarini and Braga, 1987; Bizzarini and Gnoli, 1991; Bizzarini *et al.*, 1986; Bandel, 1994; Neri *et al.*, 1995; Stanley and Swart, 1995). The ceratites at our disposal are pyritized steinkerns with parts of their original aragonitic shell preserved.

Specimens were mechanically broken down using needles and snippers and selected fragments were then mounted on stubs for scanning electron microscopy (SEM). The terminology of the ammonitella is reviewed in Landman *et al.* (1996). Approximately 15 specimens were examined, six of which are described in this paper. They are reposited in the American Museum of Natural History (AMNH) and the Museo Civico di Storia Naturale di Venezia (MCSNV).

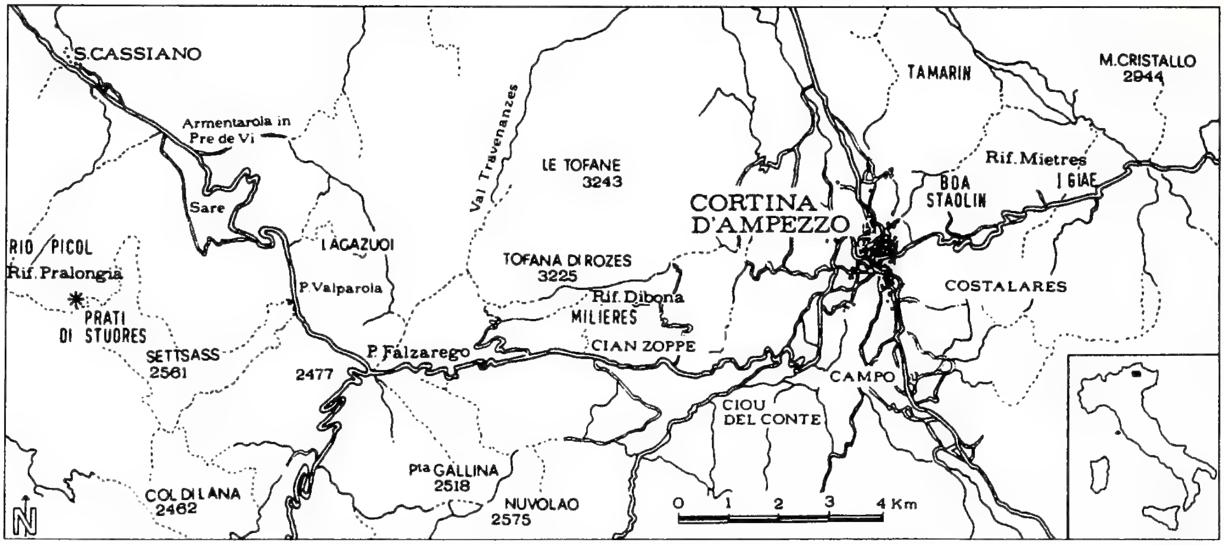
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Fig. 1. Map of the general area in Italy in which the specimens were collected (elevations in meters). The best preserved material comes from Prati di Stuores (asterisk, western edge of the map).

RESULTS

The ceratites studied display a tuberculate micro-ornamentation on their ammonitellas. The tubercles are approximately 4 µm in diameter and disappear at the ammonitella edge. This micro-ornamentation is illustrated in AMNH 46594-46597.

AMNH 46594, *Trachyceras* cf. *Trachyceras (T.) aon*, preserves a small patch of outer shell on the first whorl of the ammonitella (Fig. 3A). At high magnifications (500x, 1000x), tubercles are visible on the shell surface (Fig. 3B, C). They are irregularly distributed, although it is not uncommon for three or four tubercles to form a short row (Fig. 3C). The tubercles are approximately 4 µm in diameter and 2 µm in height (Fig. 3D-F).

The wall of the ammonitella appears to consist of three prismatic layers, which total approximately 11 µm in thickness (Fig. 3D). The outermost layer is 1-2 µm thick. The prisms in this layer are approximately 1.5 µm in diameter and seem to be arranged in longitudinal rows (Fig. 3C). These prisms are organized into larger units, approximately 4 µm in diameter, which represent pseudohexagonal trillings (= three cyclically twinned crystals forming a hexagon) (Fig. 3E, F). The tubercles are extensions of the pseudohexagonal trillings and are composed of multiple sectors (Fig. 3E, F).

In AMNH 46595, *Trachyceras (Brotheotrachyceras) larva*, part of the shell wall is preserved at the primary constriction (Fig. 4A). Tubercles are visible on the adapical side of the deepest part of the constriction (Fig. 4B, C). They are approximately 4 µm in diameter (Fig. 4D). They are sparsely and irregularly distributed and are part of the

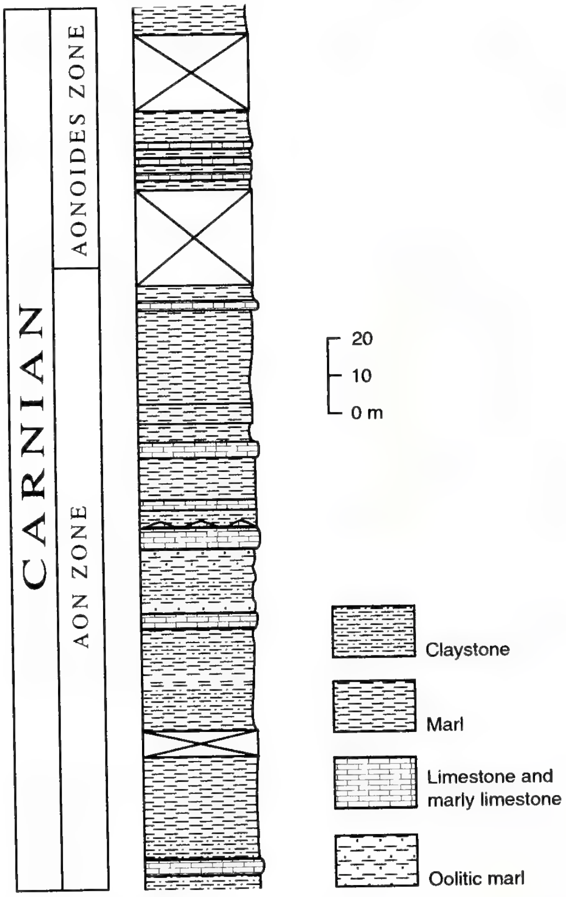
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Fig. 2. Generalized stratigraphic section of the Upper Triassic (Carnian) San Cassiano Formation at Prati di Stuores. The ammonites studied occur throughout the section. The Aon and Aonoides Zones are ammonite biozones.

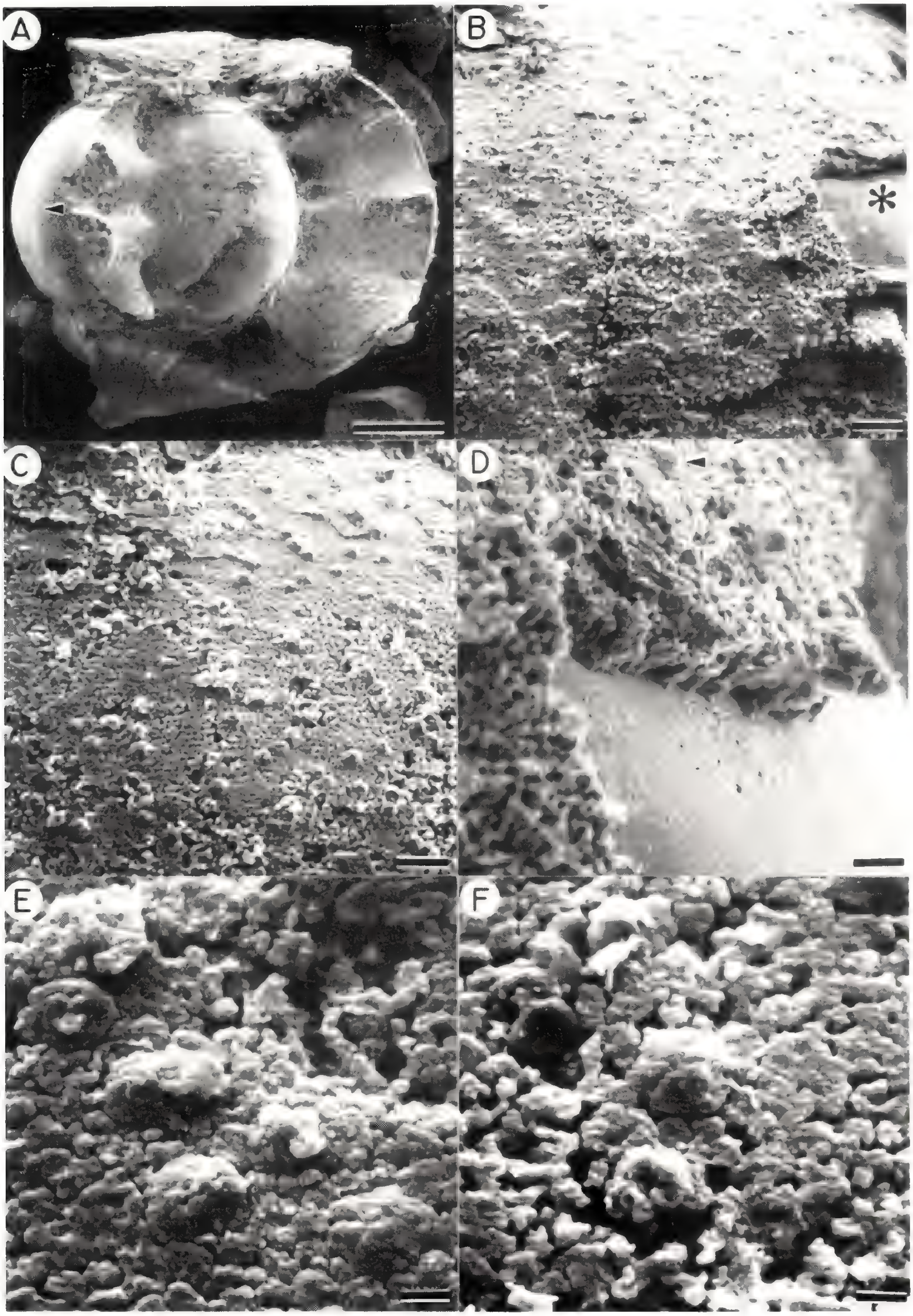

Fig. 3. *Trachyceras* cf. *Trachyceras (T.) aon* (Münster, 1834), AMNH 46594, San Cassiano Formation, Dolomites, Italy. A. Ventral view of the first whorl of the ammonitella and the primary constriction (arrow). Scale bar = 200 μm. B. Close-up of a patch of shell with tubercles. The adoral direction is toward the right. The asterisk indicates the position of D. Scale bar = 20 μm. C. The tubercles are densely and randomly distributed. Note the longitudinal arrangement of the prismatic crystals. Scale bar = 10 μm. D. Close-up of a broken part of the shell wall showing three prismatic layers. The outermost layer is covered with tubercles (arrow). Scale bar = 5 μm. E. The tubercles are extensions of pseudohexagonal trillings. Scale bar = 2 μm. F. The outer layer is composed of prismatic crystals oriented perpendicular to the surface. Scale bar = 2 μm.

outer prismatic layer. A nacreous layer is visible at some depth below the outer prismatic layer and represents the nacre of the primary varix (Fig. 4C).

AMNH 46596, *Trachyceras (Trachyceras) aon*, also preserves a patch of shell wall on the ammonitella near the primary constriction (Fig. 5A). The shell is covered with irregularly distributed tubercles (Fig. 5B). The prisms of the outer layer are visible on the shell surface, especially where the surface is eroded (Fig. 5C, left side). The tubercles are approximately 4 µm in diameter and are composed of multiple sectors converging to a conical top (Fig. 5D). In some areas, the tubercles are missing, leaving depressions in the outer layer (Fig. 5D, right side). The tubercles become slightly smaller and disappear near the end of the primary constriction (Fig. 5E, F).

The best specimen is AMNH 46597, *Trachyceras (Trachyceras) aon.* Tubercles cover the entire exposed surface of the ammonitella but are better developed on the first whorl than on the initial chamber (Fig. 6A). The tubercles are densely and irregularly distributed (Fig. 6A-C). Each tubercle is approximately 4 µm in diameter with an hexagonal outline (Fig. 6D). The tubercles disappear at the

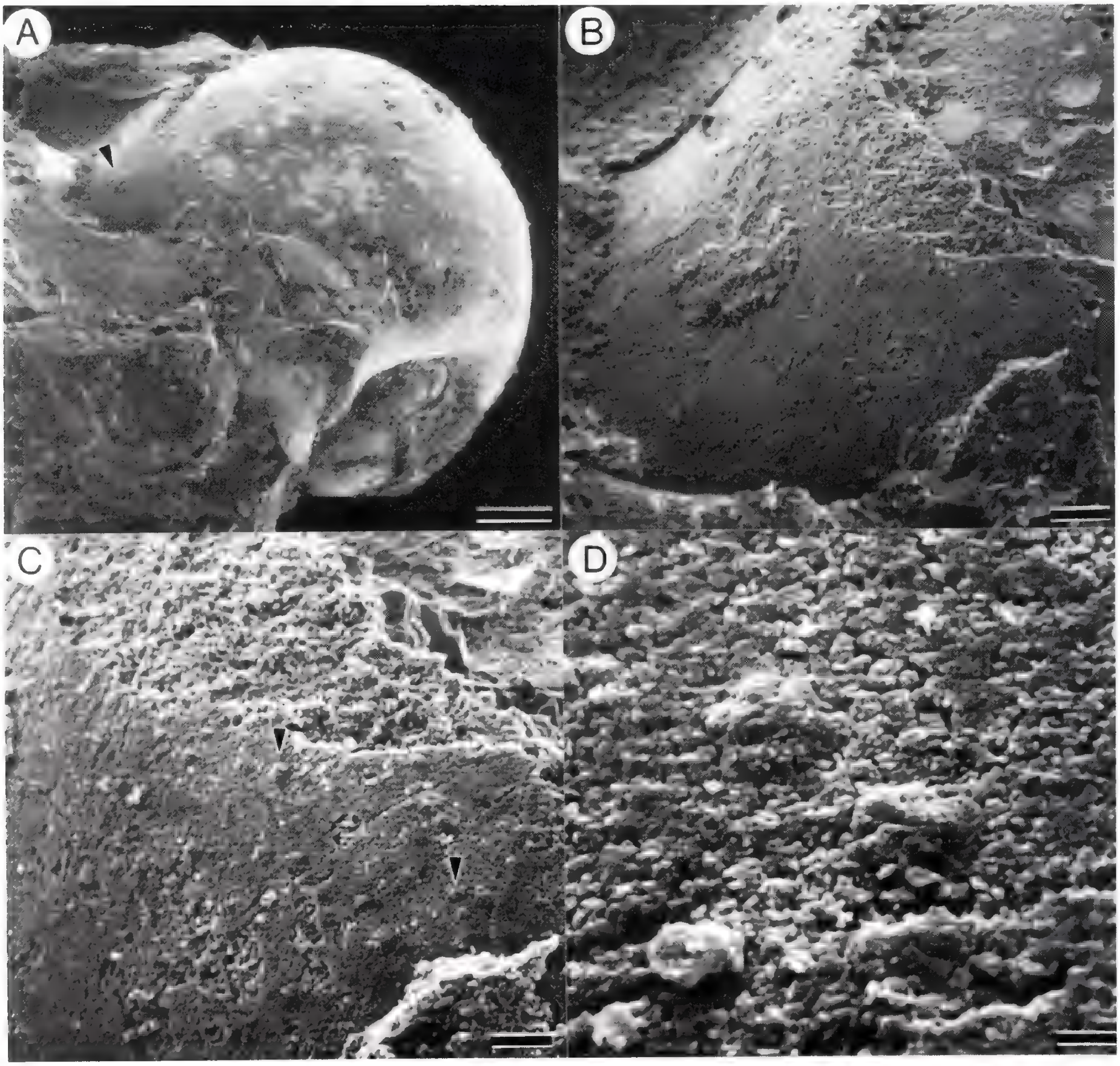

Fig. 4. *Trachyceras (Brotheotrachyceras) larva* (Klipstein, 1843), AMNH 46595, San Cassiano Formation, Dolomites, Italy. A. Ventral view of the adoral end of the ammonitella showing the primary constriction (arrow). Scale bar = 100 µm. B. Close-up of the primary constriction. Scale bar = 20 µm. C. The tubercles (arrows) are visible on the adapical part of the primary constriction. Scale bar = 10 µm. D. Close-up of the tubercles, which appear to be extensions of pseudohexagonal trillings. Scale bar = 2 µm.

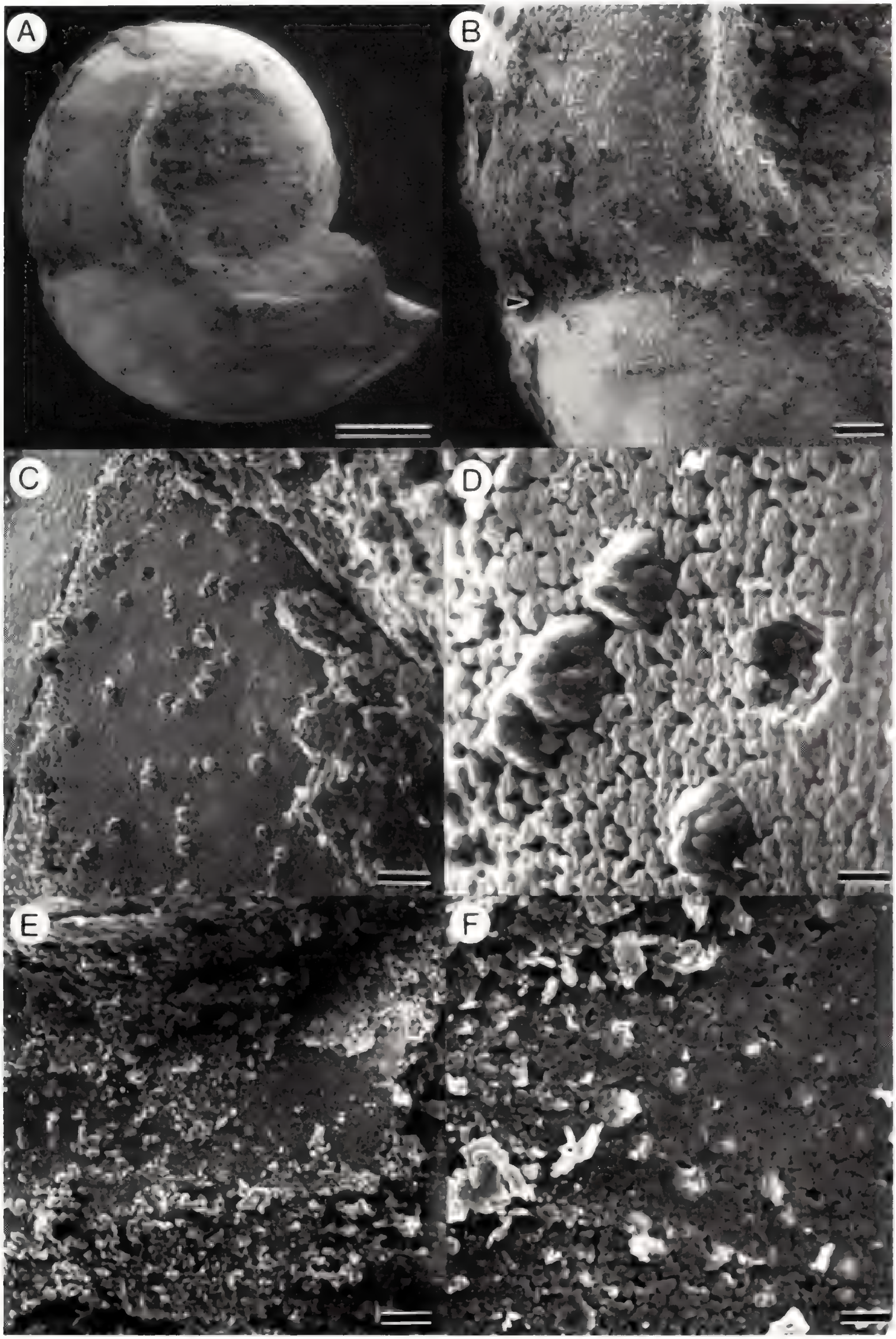

Fig. 5. *Trachyceras (Trachyceras) aon* (Munster, 1834), AMNH 46596, San Cassiano Formation, Dolomites, Italy. A. Right lateral view of the ammonitella and part of the first whorl. Scale bar = 200 µm. B. A patch of shell is visible on the adoral end of the ammonitella near the primary constriction (arrow). Scale bar = 50 µm. C. The tubercles are irregularly distributed on the shell surface. The specimen has been rotated 30° clockwise relative to A. Scale bar = 10 µm. D. The tubercles are composed of multiple sectors converging to a conical top. Scale bar = 2 µm. E. Close-up of the shell surface at the primary constriction. The adoral direction is toward the right (same orientation as C, D). Scale bar = 20 µm. F. The tubercles disappear in the adoral direction (toward the right) in the primary constriction. Scale bar = 5 µm.

ammonitella edge, which is very well defined in this specimen (Fig. 6E, F). The postembryonic shell shows a series of discontinuous, transverse lirae composed of interconnected tubercles (Fig. 6E, left arrow).

Micro-ornamentation is also present on the postembryonic whorls of these ceratites and consists of ridges and tubercles aligned in longitudinal rows. This micro-ornamentation is illustrated in AMNH 46598 and AMNH 46599.

In AMNH 46598, *Trachyceras* cf. *Trachyceras (T.) aon*, there is a piece of the postembryonic shell wall on the left side of the specimen (Fig. 7A). Micro-ornamentation covers the whole flank from one umbilical seam to the other, but is less distinct on the inner two thirds of the flank than on the outer one third of the flank (Fig. 7B). The micro-ornamentation consists of ridges and tubercles arranged in longitudinal rows. The ridges and tubercles form a broad concavity on the inner two-thirds of the flank and are straight and prorsiradiate on the outer one third of the flank. The ridges and tubercles occur on a porous spicular surface. Large crystallites are visible where this surface is eroded (Fig. 7C, lower left). The surface is free of growth lines (Fig. 7C) although faint ribs and a marked growth discontinuity (Fig. 7B, asterisk) are present on the outer flank.

There is some variation in the shape of the ridges and tubercles on the postembryonic shell. Some elements are symmetric but most have an asymmetric profile with a steeply sloping adoral face and a more gently sloping adapical face. The tubercle on the right side in Fig. 7D is approximately 10 µm in length.

The micro-ornamentation on the postembryonic shell is beautifully preserved in AMNH 46599, *Trachyceras (Trachyceras) muensteri* (Fig. 8). This specimen consists of half a postembryonic whorl broken off of a larger specimen. The ammonitella is completely covered up. On the adapical end of the fragment, the micro-ornamentation is present on a patch of outer shell and extends from the umbilical seam to the right side of the mid-venter (Fig. 8A). The micro-ornamentation consists of tubercles and ridges aligned in longitudinal rows (Fig. 8A, B). The tubercles and ridges follow a prorsiradiate pattern on the outer flanks.

The tubercles are asymmetric in shape and seem to be composed of several sectors. They are approximately 8 µm in diameter and approximately 4 µm in height (Fig. 8C, left side). They are developed on a thin prismatic layer approximately 2 µm thick. The prismatic crystals composing this layer seem to be organized into pseudohexagonal trillings (Fig. 8C, upper right). Growth lines are absent although viewed from a low angle, the surface shows a series of undulations, each approximately 10 µm in width, oriented perpendicular to the direction of growth (Fig. 8A).

On the adoral portion of this specimen, micro-ornamentation is preserved on the venter and flanks (Fig. 8D). It consists of ridges and tubercles aligned in longitudinal rows (Fig. 8E). The individual ridges are elongated in a longitudinal direction; the ridge in Fig. 8F is 20 µm long.

DISCUSSION

The ammonitellas of these ceratites are covered with tubercles, each approximately 4 µm in diameter. The tubercles occur on the exposed portions of the ammonitella and disappear at the ammonitella edge. They seem to be extensions of pseudohexagonal trillings in the outer prismatic layer. They form an integral part of this layer as indicated by the presence of depressions where individual tubercles have broken off (Fig. 5D).

The shape, size, distribution, and microstructure of these tubercles indicate that they are homologous to those reported on the ammonitellas of other Mesozoic suborders, namely Lytoceratina, Phylloceratina, Ancyloceratina, and Ammonitina, known collectively as the Ammonitida (see, for example, Brown, 1892, pl. 9, fig. 4; Kulicki, 1974, pl. 4, fig. 1; Kulicki, 1979, pl. 48, fig. 3; Kulicki, 1996, figs. 4D, 5E, F; Kulicki and Doguzhaeva, 1994, fig. 11D, F; Bandel, 1982, pl. 13, figs. 1, 6, 7; Bandel *et al.*, 1982, figs. 1, 2; Landman, 1985, fig. 2B; Landman, 1987, fig. 4; Landman, 1988, fig. 1; Landman, 1994, figs. 2, 3; Landman and Waage, 1993, figs. 13, 14; Landman *et al.*, 1996, figs. 12, 13; Tanabe, 1989, figs. 1-3, 4C, D; Sprey, in press, fig. 3A). This micro-ornamentation differs from that on the ammonitellas of Paleozoic ammonoids, which are covered by transverse lirae in the Agoniatitina, Anarcestina, and Tornoceratina, and are smooth in the Goniatitina (Landman *et al.*, 1996; for goniatites, see Kulicki *et al.*, in press, b). The presence of the same micro-ornamentation on the ammonitellas of Mesozoic ammonoids may represent a synapomorphy for this group.

The size and morphology of the tubercles vary slightly among Mesozoic ammonoid suborders, possibly providing useful characters for phylogenetic analysis. In the Ceratitina, the tubercle size averages 4 µm based on several specimens of *Trachyceras*. In the Ammonitina, the tubercle size ranges from 2-4 µm based on a sample of seven genera (*Anapachydiscus, Metaplacenticeras, Desmophyllites, Quenstedtoceras, Kosmoceras, Aconeceras*, and *Binatisphintes*) (see above references). In the Phylloceratina, the tubercle size averages 3 µm in a single specimen of *Hypophylloceras* (see Tanabe, 1989, fig. 2D). In contrast, the tubercle size is larger in the Lytoceratina and Ancyloceratina. It ranges from 3.5-7 µm in two genera of Lytoceratina (*Gaudryceras* and *Anagaudryceras*), and 4.5-7.5 µm in five genera of Ancyloceratina (*Scaphites, Hoploscaphites, Clioscaphites, Jeletzkytes*, and *Discoscaphites*) (see above references).

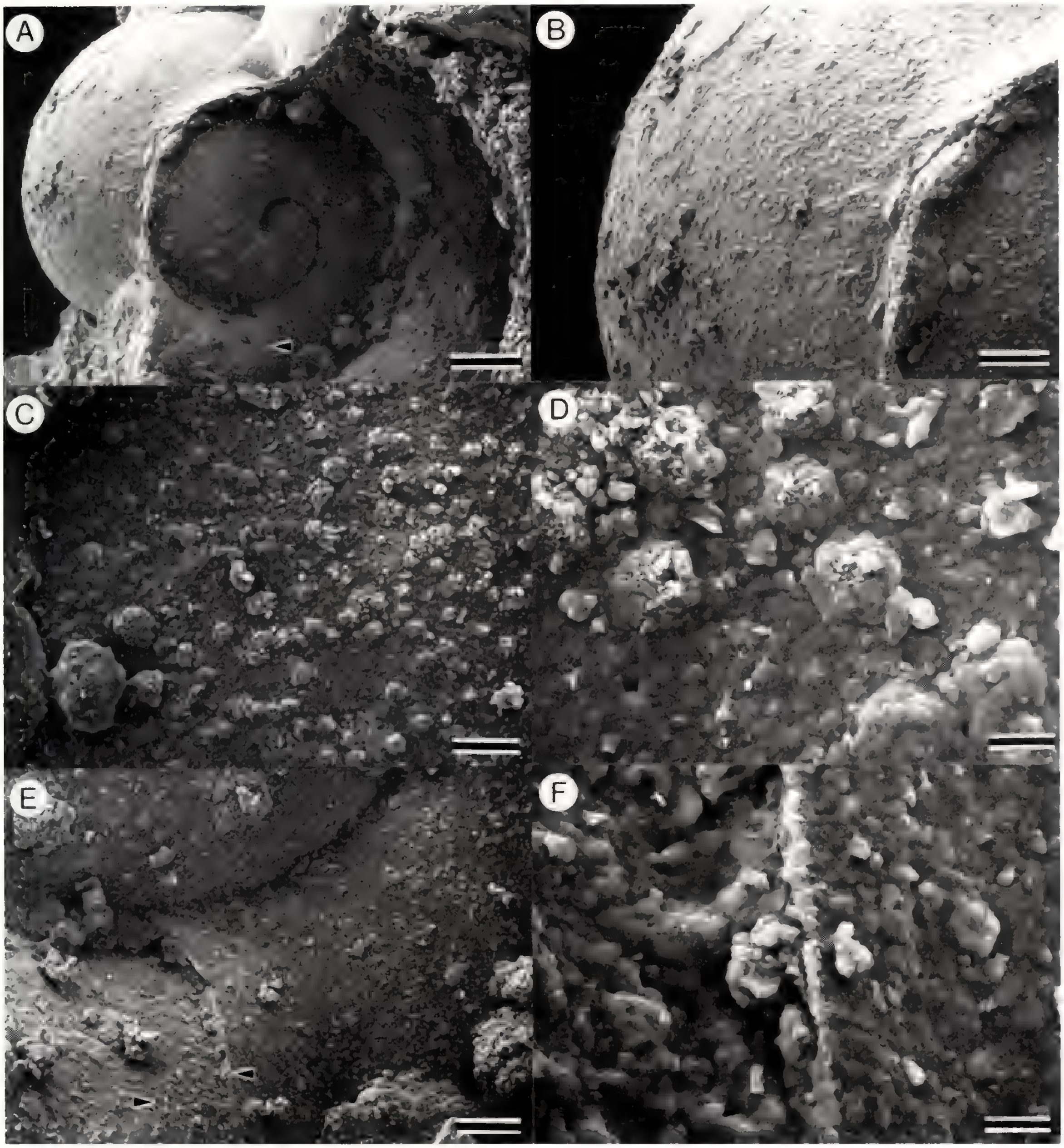

Fig. 6. *Trachyceras (Trachyceras) aon* (Münster, 1834), AMNH 46597, San Cassiano Formation, Dolomites, Italy. A. The postembryonic whorls have broken off exposing the ammonitella and ammonitella edge (arrow). The remnant of the umbilical seam of the succeeding whorl is still attached. Scale bar = 115 μm. B. The ammonitella is covered with tubercles. Scale bar = 50 μm. C. The tubercles are densely and irregularly distributed on the shell surface. Scale bar = 15 μm. D. Close-up of the tubercles. Scale bar = 3 μm. E. The ammonitella edge (right arrow) is sharply defined. Note the micro-ornamentation (left arrow) on the postembryonic shell. Scale bar = 30 μm. F. Close-up of the ammonitella edge. Scale bar = 3 μm.

Another source of variation is the distributional pattern of tubercles on the shell surface, but it is difficult to determine how much of this variation is due to differences in preservation. For example, Tanabe (1989, fig. 2C) noted in some species that the density of tubercles on the first whorl of the ammonitella is greater nearer the umbilical seam with the next whorl than on the rest of the flanks. Tanabe (1989, fig. 1A) also noted that tubercles sometimes form a continuous layer on the umbilical wall of the initial chamber even though they are distinct on the rest of the ammonitella. In our ceratites, the tubercles are generally uniformly distributed on the shell surface, although in AMNH 46597, the tubercles are less densely distributed on the initial chamber than on the first whorl.

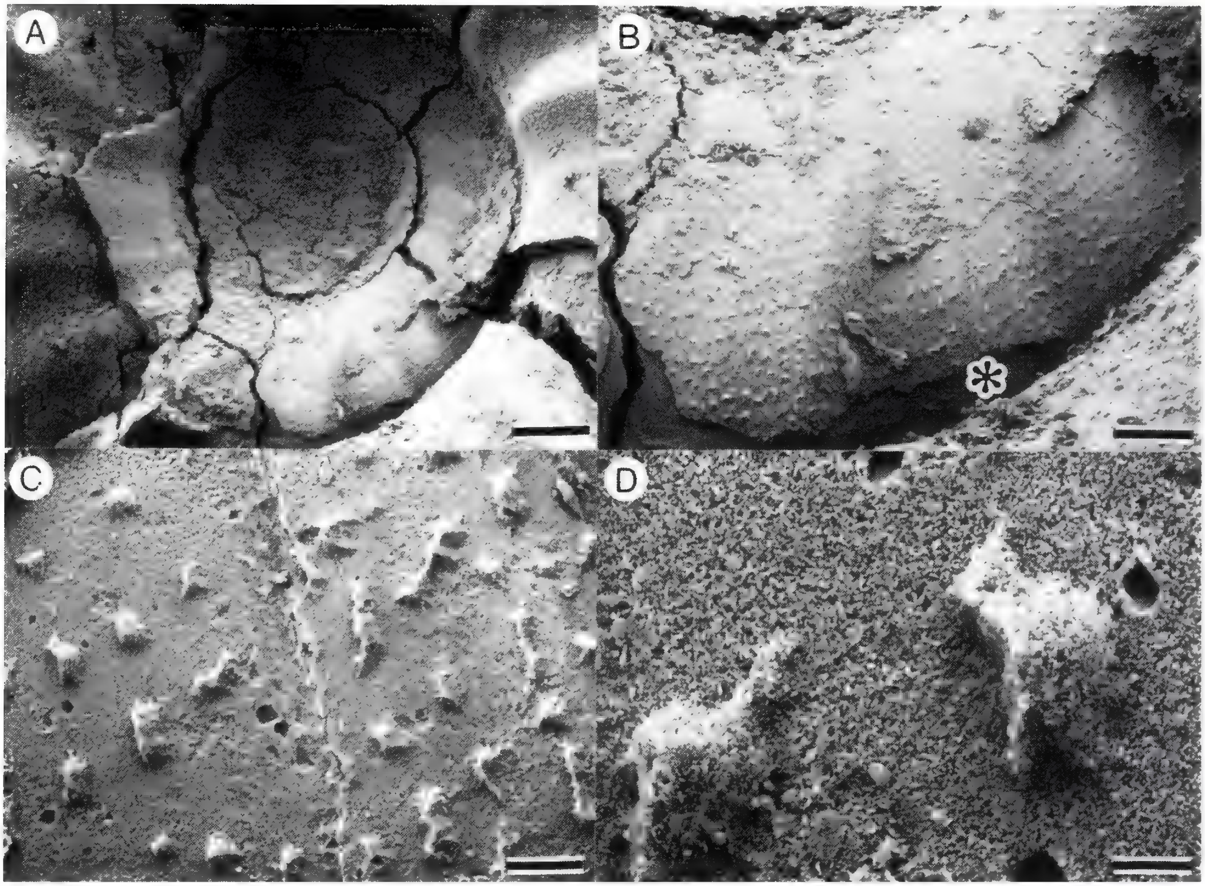

Fig. 7. *Trachyceras* cf. *Trachyceras (T.) aon* (Münster, 1834), AMNH 46598, San Cassiano Formation, Dolomites, Italy. A. Overview of the early postembryonic whorls. The ammonitella is not exposed. Scale bar = 215 µm. B. The micro-ornamentation consists of tubercles and ridges aligned in longitudinal rows. Note the growth discontinuity (asterisk). Scale bar = 75 µm. C. Close-up of tubercles and the growth discontinuity. The adoral direction is toward the left. Scale bar = 15 µm. D. The tubercle on the right has an asymmetric profile with a gently sloping adapical face and a more steeply sloping adoral face. The adoral direction is toward the left. Scale bar = 3 µm.

A further source of variation is tubercle microstructure, although this variation, again, might principally be due to differences in preservation. For example, the tubercles in scaphitid ammonoids appear to be monolithic (see, for example, Tanabe, 1989, figs. 2D, 3A; Landman and Waage, 1993, fig. 13F) whereas those in other ammonoids such as *Quenstedtoceras* are clearly composed of multiple sectors (see Bandel *et al.*, 1982, fig. 2C). In most of our specimens of *Trachyceras*, the tubercles are extensions of pseudohexagonal trillings in the outermost prismatic layer and consist of multiple sectors (Fig. 3F).

The absence of growth lines on the surface of all ammonitellas indicates that the embryonic shell was secreted in uninterrupted contact with the gland cells of the mantle. However, the mode of formation of the tubercles is still unknown. There are two competing hypotheses. Bandel (1982, 1986) suggested that the ammonitella of Mesozoic ammonoids initially consisted of an organic, unmineralized shell with tubercles. He argued that this shell was mineralized by prismatic needles from the inside, preserving its original micro-ornamentation. Tanabe (1989) proposed an alternative model in which the mode of embryonic development switched from ectocochliate to endocochliate, and then back to ectocochliate late in embryogenesis. According to this model, the outer mantle reflexed back onto the outside of the ammonitella during the endocochliate stage, secreting the outer prismatic layer and tuberculate micro-ornamentation.

The micro-ornamentation on the postembryonic shells of these ceratites consists of ridges and tubercles aligned in longitudinal rows. In some specimens, the ridges and tubercles follow a concave pattern on the inner flanks and a straight, prorsiradiate pattern on the outer flanks. This ornamentation occurs on a thin prismatic layer on both the venter and flanks.

Our data suggest that there is an ontogenetic change in the appearance of this micro-ornamentation. In early postembryonic growth, the micro-ornamentation consists of discontinuous, transverse lirae composed of interconnected tubercles (Fig. 6E, left arrow). During ontogeny, the network of tubercles becomes more distinct, and the tubercles themselves become more ridge-like (Fig. 8A, D, F). In still later ontogeny, it is possible that these ridges unite to form longitudinal striae.

A similar micro-ornamentation has been documented in three genera of Jurassic ammonites including *Quenstedtoceras* (see Kulicki, 1974, pl. 4, figs. 1, 2), *Kosmoceras* (see Kulicki, 1979, pl. 48, fig. 4; Sprey, in press, fig. 1), and *Binatisphinctes* (see Sprey, in press, figs. 2, 3B). The micro-ornamentation consists of tubercles and ridges aligned in longitudinal and transverse rows in *Quenstedtoceras* and *Kosmoceras* and in longitudinal and prorsiradiate rows in *Binatisphinctes*. In all three genera, the ridges and tubercles occur on a thin prismatic layer marked by occasional growth lines.

This micro-ornamentation is reminiscent of the tuberculate micro-ornamentation on the ammonitella but there are many differences. The tubercles on the postembryonic shell are larger and more asymmetric than those on the ammonitella. The tubercles on the postembryonic shell are also aligned in longitudinal rows, whereas they are irregularly distributed on the ammonitella. In addition, growth lines or growth discontinuities are present on the surface of the postembryonic shell, whereas they are absent on the ammonitella.

The micro-ornamentation on these postembryonic shells resembles the wrinkle layer, which is secreted as part of the dorsal wall (Walliser, 1970; House, 1971; Senior, 1971; Tozer, 1972; Kulicki, 1979; Kulicki *et al.*, in press, a). This layer generally covers the surface of the preceding whorl and extends some distance adoral of the aperture. It forms a wide variety of patterns (Walliser, 1970, fig. 3), although none of these patterns exactly matches the micro-ornamentation described here. Nevertheless, the asymmetric profile of many of the tubercles on these ceratites, with a gently sloping adapical face and a more steeply sloping adoral face, is characteristic of the elements of the wrinkle layer (Kulicki, 1979, fig. 9).

Tozer (1972, p. 642) noted spiral ornamentation in the Triassic ceratite *Discotropites* and cited a specimen of *Discotropites laurae* (Mojsisovics, 1893) illustrated by Smith (1927, pl. 11, fig. 8) that displayed this feature. A similar ornamentation also occurs in *Amaltheus* (see Zittel, 1924, p. 575, fig. 1218; Walliser, 1970, pl. 4, fig. 5). However, unlike the micro-ornamentation described here, the ornamentation in both of these genera consists of only spiral ridges, not tubercles, and Tozer (1972, p. 643) considered both of them to have been secreted as part of the dorsal wall.

Despite the superficial resemblance to the wrinkle layer, the micro-ornamentation on the postembryonic shells of our ceratites probably did not form as part of the dorsal wall. If the micro-ornamentation had been secreted by a supracephalic mantle fold, this ornamentation would have covered the boundary between the ammonitella and postembryonic shell. Instead, the micro-ornamentation appears abruptly at the start of the postembryonic shell.

It is more likely that the postembryonic micro-ornamentation formed at the apertural margin. The tubercles were probably secreted at specific sites along the mantle edge. As the shell grew, the tubercles formed a series of longitudinal rows. The micro-ornamentation on the shell probably reflected that of the periostracum. A similar phenomenon has been observed in modern *Nautilus* in which spherical bundles of crystals form at the growing edge of the mantle at the intersection of spiral and radial lirae (see Arnold *et al.*, 1987, fig. 7). These lirae reflect the ornamentation of the periostracum.

FUTURE WORK

It is important to examine members of other ceratite families to determine if they also display a tuberculate micro-ornamentation on the ammonitella. Previous studies (Landman *et al.*, 1996) have suggested that the kind of micro-ornamentation on the ammonitella is invariant at the subordinal level. However, additional sampling is recommended. Along the same lines, we need to examine members of other suborders in which the micro-ornamentation on the ammonitella is still unknown. The most notable omission is the Prolecanitina, which is presumed to be ancestral to the Mesozoic ammonoids (House, 1988, Text Fig. 4). Lastly, we need to evaluate the variation in tuberculate micro-ornamentation among Mesozoic suborders to develop a set of character states useful for investigating relationships within this group. Such character states may include the size, microstructure, and distribution of tubercles on the shell surface.

The mode of formation of the micro-ornamentation on the postembryonic shell is puzzling. To resolve this issue, it is important to document other occurrences of this micro-ornamentation. Does this micro-ornamentation occur at the apertural margin in specimens with preserved apertures? Does a dorsal shell layer also cover the preceding whorl? The presence of the same micro-ornamentation in three genera of Jurassic Ammonitina and one genus of Triassic Ceratitina suggests that it is widespread. Does it occur in still other genera?

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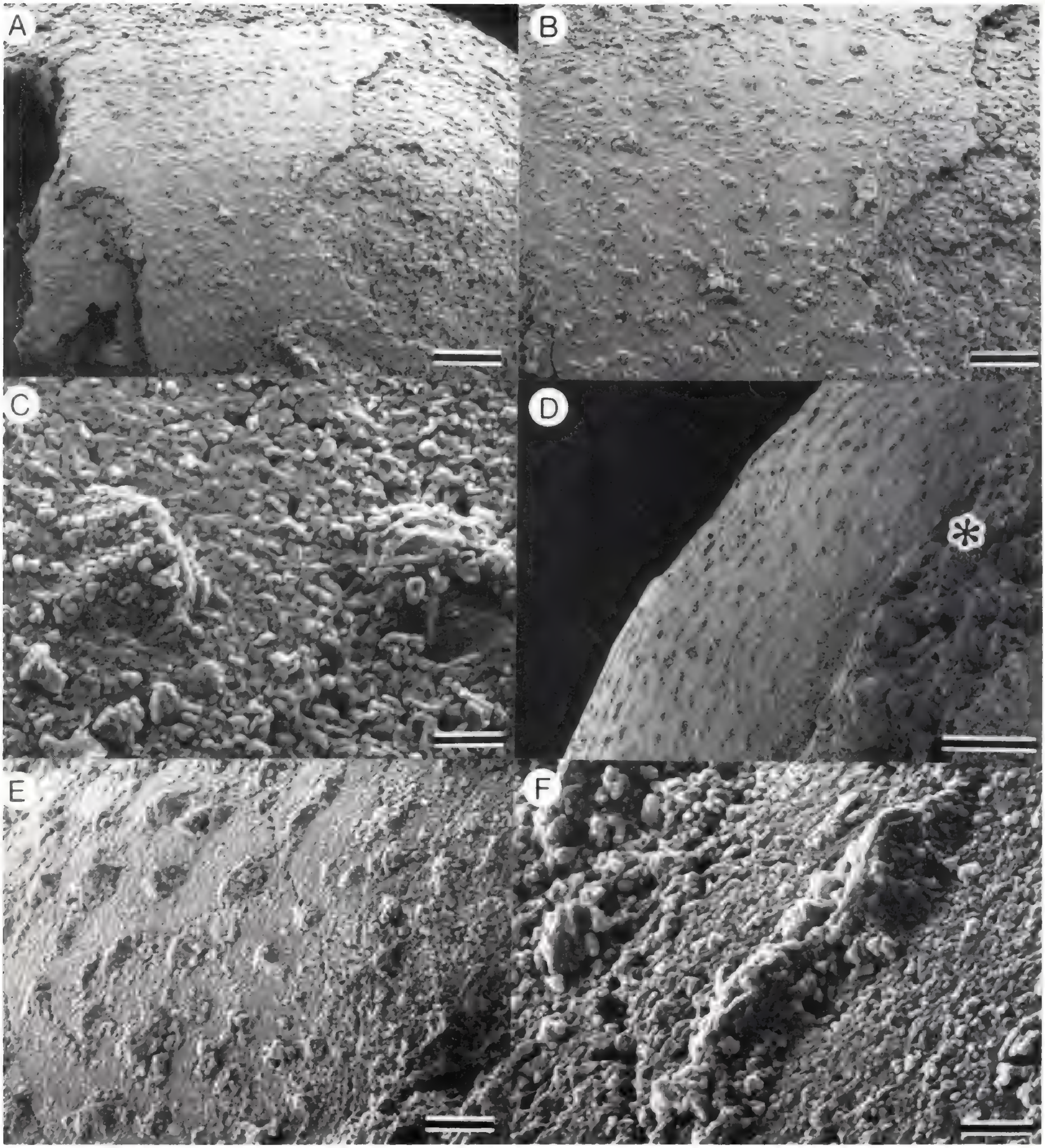

Fig. 8. *Trachyceras (Trachyceras) muensteri* (Wissmann, 1841). AMNH 46599, San Cassiano Formation, Dolomites, Italy. A. The micro-ornamentation is visible on the early postembryonic shell. The adoral direction is toward the right. Scale bar = 60 µm. B. The tubercles are aligned in longitudinal rows. The adoral direction is toward the right. Scale bar = 30 µm. C. The tubercle on the left has an asymmetric profile with a gently sloping adapical face and a more steeply sloping adoral face. The adoral direction is toward the right. Scale bar = 3 µm. D. Overview of the same specimen one-third whorl adoral of A. The adoral direction is toward the upper right. The asterisk indicates the position of E. Scale bar = 60 µm. E. No growth lines are visible on the surface of the shell. Scale bar = 15 µm. F. Close-up of a ridge elongated in the longitudinal direction. Scale bar = 3 µm.

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Puperita tristis (d'Orbigny, 1842) (Gastropoda: Neritidae) is an ecotype of *Puperita pupa* (Linnaeus, 1767)

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Abstract: *Puperita pupa* and *P. tristis* occur sympatrically in the West Indies. In his 1941 review of western Atlantic Neritidae, Russell kept the two species separate based on shell color differences: *P. pupa* is characterized by a white shell with black lines, *P. tristis* by a black shell with small white spots. Russell also included radula differences, but noted that both species exhibit plasticity for both characters. Authors have suggested that *P. tristis* is a variety or color form of *P. pupa*. We tested the relationship of *P. pupa* and *P. tristis* through examinations of shell and radular characters, reciprocal translocations, and random amplified polymorphic DNA (RAPD). *P. pupa* and *P. tristis* do not differ significantly in shell shape and proportion, as measured by principal component analysis. Translocations showed that the *pupa* and *tristis* phenotypes could be expressed by either nominal species. No radular differences were seen between the two putative species. Statistical analysis of RAPD band sharing indicated that interspecific variation did not differ significantly from intraspecific variation, and that *Puperita* is separate from *Neritina*. Considering our findings, we believe *P. pupa* and *P. tristis* to be conspecific, with *P. tristis* an ecotype of *P. pupa*. Shell color pattern appears to be responding to environmental conditions. An unusual feature of this plasticity is the sudden and dramatic change in shell phenotypes in response to a change in habitat.

Key Words: phenotype, plasticity, RAPD, Neritidae, radula

Puperita pupa (Linnaeus, 1767) and *P. tristis* (d'Orbigny, 1842) (Gastropoda: Neritidae) are two nominal species of supralittoral gastropod occurring sympatrically in the West Indies. Russell (1941) provided the only complete treatment of these species using color pattern and differences in radula morphology to separate the species. Both species exhibit plasticity in shell pattern. The black lines of *P. pupa* may vary greatly in number and size, and may outline certain areas, giving an irregular spotted appearance (Russell, 1941). The white spots of *P. tristis* vary in number and size, occasionally forming three to four transverse bands near the suture and umbilicus (d'Orbigny, 1842). Russell (1941) notes that while shell patterns of these species are normally distinct from each other, intergrades occur. For example, *P. pupa* taken from certain areas in Florida possess a unique, scaled pattern resembling a cross between *P. pupa* and *P. tristis* (Fig. 1C). Both species exhibit similar shell characteristics, such as overall shape and palatal and parietal lip features. Radulae of *P. pupa* and *P. tristis* differ only in the degree of cusping of the E-lateral tooth (Russell, 1941), which in *P. tristis* tends to be more distinctly cusped than in *P. pupa*.

Puperita tristis has been considered a synonym (Tryon, 1888) and a form (Abbott and Dance, 1986) of *P. pupa*. Some classifications (Abbott, 1974) maintain *P. tristis* as a full species, but note that it may be a variety of *P. pupa*. With the exception of Russell's work, there have been few examinations of relationships between these species. In this paper, the relationship between *P. pupa* and *P. tristis* is studied by shell and radula examination, reciprocal translocation of individuals from both species, and RAPDs.

The method of randomly amplified polymorphic DNA (RAPD) markers was developed by Williams *et al.* (1990) and Welsh and McClelland (1990), and has applications in molecular ecology (Hadrys *et al.*, 1992) including differentiating between closely related individuals (Smith *et al.*, 1992), populations (Hu and Quiros, 1991), and species (Kambhampati *et al.*, 1992). In essence, segments of genomic DNA are amplified by the polymerase chain reaction (PCR) using random length primers whose sequence might appear numerous times within a genome. The RAPD amplification of genomic DNA yields a set of various fragments, their number and size depending on the frequency of the primer sequence in the genome, as well as the distances between primer sites. The RAPD technique has been used successfully in mollusks to infer relationships (Crossland *et al.*, 1993; Adamkewicz and Harasewych, 1994; Pfenninger *et al.*, 1995; Stothard and Rollinson, 1996; Armbruster, 1997; Stothard *et al.*, 1997).

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Phenotypic plasticity as a result of environmental factors has been well documented in mollusk systems. For example, variation in shell color due to thermal advantage has been suggested in terrestrial gastropods (Hazel and Johnson, 1990; Burla and Gosteli, 1993). Shell banding patterns and colors in *Nucella lapillus* (Linnaeus, 1758) have been attributed to wave exposure (Berry, 1983; Crothers, 1985; Etter, 1988). Population density (Kemp and Bertness, 1984), wave action (Brown and Quinn, 1988), and presence of a predator (Appleton and Palmer, 1988) also affect gastropod shell morphology. Reciprocal transplants have been used frequently to assess specific factors influencing these phenotypic changes. Using transplant studies, habitat effects on shell growth rate and form (Hinch *et al.*, 1986; Tan Tiu and Prezant, 1987) have been shown in bivalves, and phenotypic plasticity in shell pattern (Creese and Underwood, 1976), shell morphology (Johnson and Black, 1999) and radula morphology (Padilla, 1999) has been shown in marine gastropods.

METHODS

Shells and living *Puperita pupa* and *P. tristis* were collected from rocky shores adjacent to the Hofstra University Marine Lab (HUML), Priory, Jamaica, West Indies. All voucher specimens were deposited at the American Museum of Natural History, NY (AMNH 296891, 296892). Museum material was also examined (Table 1). The three measurements Russell (1941) made were taken for each shell using vernier calipers: (1) aperture diameter, measured from middle of the parietal lip to middle edge of the outer lip; (2) shell height, measured as vertical height of the body whorl; and (3) shell length, measured as horizontal distance from edge of the outer lip to end of the whorl. Juvenile shells with fewer than two whorls were excluded from study. Individuals were grouped according to species and lot where applicable. Mean aperture diameter, shell height, and shell length for each lot and species were calculated and species means compared by t-test. Size and shape differences were additionally tested by principal component analysis using Systat (SPSS, Chicago, IL).

The salinity of water samples from nine pools where both *Puperita* species were collected in Jamaica was determined as a measure of conductivity using a Corning PS-17 conductivity meter. Salinities were grouped by species presence and compared by t-test.

Two transplant experiments were conducted to test for possible environmental effects on shell phenotype. In the first experiment, *Puperita tristis* were found living in a meter deep, spring-fed brackish pool in the rocky shore at Urchin Cove, a site near HUML. Topography of the pool

Table 1. Data for self-collected and loaned specimen lots. Lot ID: AMNH - American Museum of Natural History; FLMNH - Florida Museum of Natural History; DMNH - Delaware Museum of Natural History; RWG - private collections made by the authors. n: number of individuals per lot. AP: aperture diameter, SL: shell length, SH: shell height. Measurement values are the mean ± standard deviation.

Species	Location	Lot ID	n =	AP (mm)	SL (mm)	SH (mm)
P. pupa	Bahamas	DMNH 49556	18	4.13 ± 0.43	9.13 ± 1.08	5.67 ± 0.78
	Bahamas	DMNH 49571	26	4.06 ± 0.32	8.48 ± 0.61	5.30 ± 0.37
	Bahamas	FLMNH 1834	33	4.33 ± 0.41	9.30 ± 0.92	5.90 ± 0.55
	Bimini	DMNH 49577	26	4.28 ± 0.49	9.40 ± 1.07	5.66 ± 0.70
	Cozumel	DMNH 143506	14	4.98 ± 0.27	10.76 ± 0.86	6.75 ± 0.39
	Florida	DMNH 165566	22	4.04 ± 0.40	8.81 ± 0.83	5.54 ± 0.44
	Grand Cayman	DMNH 168761	51	4.11 ± 0.44	8.81 ± 1.05	5.41 ± 0.68
	Jamaica	AMNH 296891	45	4.18 ± 0.62	9.23 ± 1.17	5.76 ± 0.89
	Jamaica	RWG	65	4.36 ± 0.45	7.76 ± 1.23	4.85 ± 0.64
	Santo Domingo	DMNH 49561	21	4.47 ± 0.26	9.73 ± 0.60	6.02 ± 0.33
	Virgin Islands	DMNH 38173	22	4.27 ± 0.31	8.97 ± 0.72	5.52 ± 0.44
	TOTAL		343	4.26 ± 0.48	8.90 ± 1.22	5.53 ± 0.76
P. tristis	Dominica Island	FLMNH 92785	68	3.62 ± 0.30	7.78 ± 0.68	4.76 ± 0.45
	Jamaica	AMNH 296892	43	4.16 ± 0.59	8.01 ± 1.34	4.95 ± 0.86
	Jamaica	DMNH 145968	19	3.65 ± 0.23	7.80 ± 0.51	4.91 ± 0.85
	Jamaica	RWG	49	3.75 ± 0.43	7.81 ± 0.75	5.29 ± 0.49
	Jamaica	RWG	24	3.95 ± 0.34	7.43 ± 0.57	5.02 ± 0.57
	Jamaica	RWG	39	4.58 ± 0.68	8.81 ± 1.41	5.42 ± 0.96
	Jamaica	RWG	13	4.21 ± 0.53	7.94 ± 1.19	4.96 ± 0.80
	Jamaica	RWG	55	4.19 ± 0.82	9.62 ± 1.88	5.84 ± 1.16
	TOTAL		310	3.99 ± 0.63	8.26 ± 1.38	5.18 ± 0.85

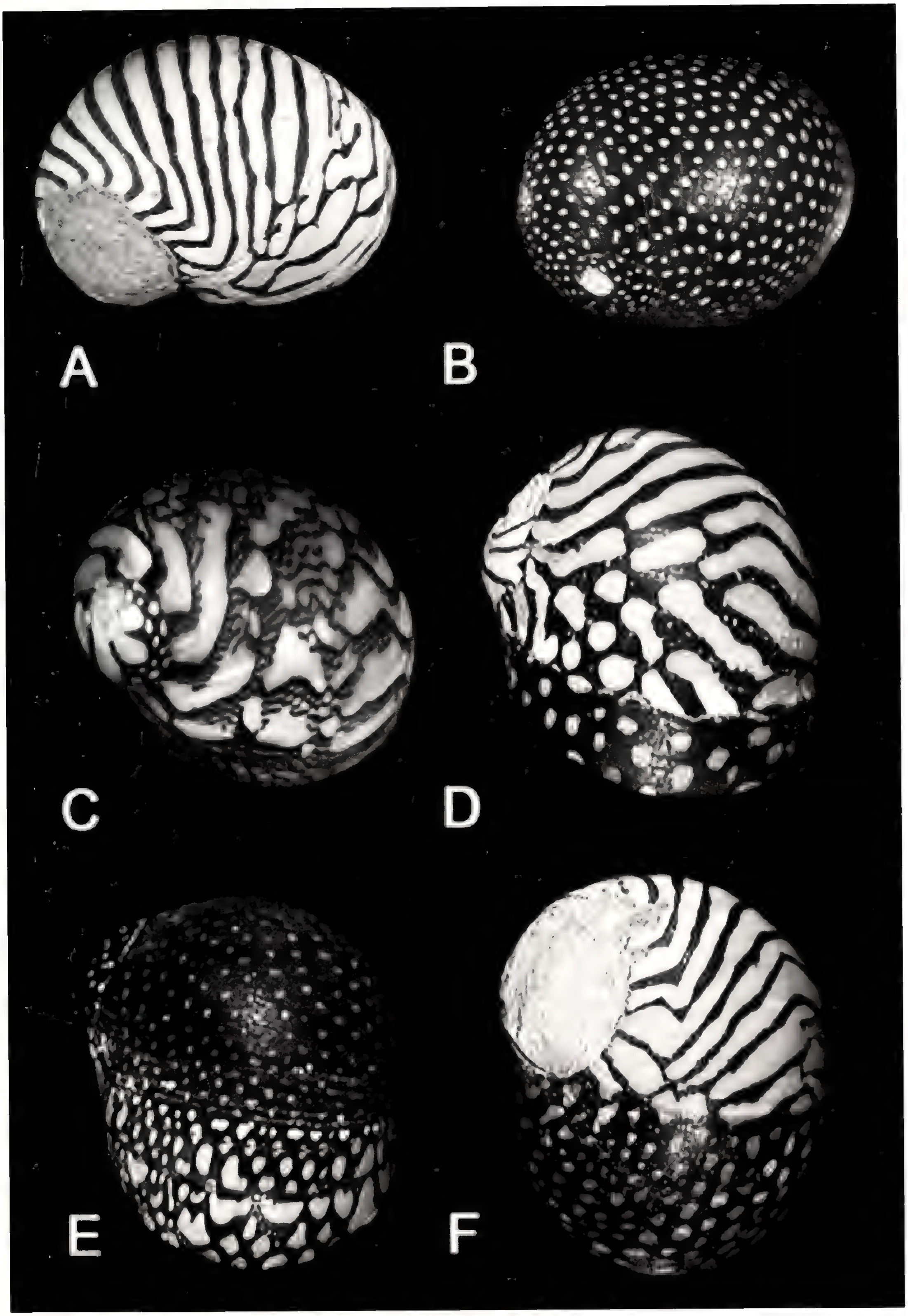

Fig. 1. *Puperita* shell phenotypes. A. *Puperita pupa*. B. *P. tristis*. Both specimens taken from pools near Hofstra University Marine Laboratory, Priory, Jamaica. C. *P. pupa* from Ohio Key, Florida. D. Translocated *P. pupa*. E. Translocated *P. tristis*. Both specimens from the three month study. F. Translocated *P. pupa* from the nine month study.

partially serves to restrict individuals within its confines. Five meters from this pool were *P. pupa* living in shallow spray pools. These pools were unprotected and potentially provided a hypervariable environment, as temperature and salinity of these pools may vary greatly (Russell, 1941). Thirty *P. pupa* and twenty *P. tristis* (adults with more than two whorls) were taken from their native pools and transplanted into the pool of the other species. Given the extreme color pattern differences between the two putative species (Fig. 1A&B), we did not believe any artificial marking of the shells to be necessary. After three months, transplanted individuals were collected and studied for any phenotypic changes. In a second experiment, thirty *P. pupa* were taken from spray pools one-quarter mile west of the experimental site and transplanted into the brackish pool. After nine months, these individuals were collected and studied (AMNH 394659).

Radulae were dissected out of preserved and transplanted individuals from both species, cleaned, and mounted following the method of Holznagel (1998). Samples were coated with gold-palladium and micrographs of the E-lateral were taken using a Hitachi S-2500 scanning electron microscope. Baker (1923) noted that the radula of the Neritidae is stable, with the most variable character being the cusps of the E-lateral.

For RAPD analysis, *Puperita pupa* and *P. tristis* were collected from Jamaica at the site previously mentioned. *P. pupa* (AMNH 296893; Fig. 1C) were also obtained from intertidal hard shores at Ohio Key, Monroe Co., Florida (24°40'N, 81°15'W). *P. tristis* were additionally collected at Jingle Beach, two miles west of Urchin Cove. *Neritina virginea* (Linnaeus, 1758; AMNH 296894) from the New Seville mangrove swamp near Priory were included as an outgroup for comparative purposes. DNA from ten individuals from each location was extracted using the method of Crossland *et al.* (1993) with the following modifications: individuals were collected in the field and preserved whole in 95% ethanol until use; tissues were rehydrated in TE (10 mM Tris, 1 mM EDTA, pH 8.0) immediately prior to extraction; and spermine and spermidine were excluded from the homogenization buffer. After extraction, samples were treated with 1 mg RNAse at 37°C for one hour, followed by precipitation as before. Samples were brought to a working concentration of 0.15 mg/ml. The RAPD protocol (Palumbi *et al.*, 1991) used 0.15 µg of genomic DNA and 0.5 units of Taq polymerase per reaction. The samples were cycled 54 times through the following PCR program: 94°C for 30 s (denaturation), 42°C for 30 s (annealing), and 68°C for one minute (extension) using nine random sequence ten base primers (Genosys Gen3-80, The Woodlands, TX). Resulting PCR products were visualized on 1.3% agarose gels in TBE (89 mM Tris, 89 mM boric acid, 2 mM EDTA). Ethidium bromide was added to the gels and running buffer to a concentration of 0.5 (µg/ml.

RAPD band fingerprints from each individual were first compared to the nine other individuals for that species and location. An average percent difference (APD) was calculated as the total number of unshared bands divided by the total number of bands present for the comparisons. Each individual was then compared to the ten individuals from the other species and locations, and a second set of APDs were calculated. The comparisons were made in respect to each primer, such that PCR products of one species or location derived from a given primer were compared to those of another species or location for that same primer. All APDs were analyzed using the Tukey test to determine whether between location differences were significant.

RESULTS

Mean shell measurements by lot and species are shown in Table 1. There were significant differences between the nominal species (t-test, $p < 0.0001$), indicating that *Puperita pupa* was about seven percent larger than *P. tristis*. Principal component analysis produced three components. The first component accounted for 87% of variance and supported ($p < 0.0001$) differences in overall shell size between the two species. The second (aperture diameter versus shell size) and third (shell height to shell length) components showed no significant differences ($p = 0.2376$ and $p = 0.183$ respectively). Additionally, there was an apparent relationship between shell color pattern and salinity. *P. pupa* were found in pools of relatively high salinity (mean = 37.45 ± 1.59 ppt), while *P. tristis* were found in pools of relatively low salinity (mean = 8.77 ± 1.58 ppt).

In the first transplant experiment, both species exhibited changes in their shell pattern (Fig. 1D&E). *Puperita tristis* transplanted into spray pools possessed the typical black with white dot phenotype, except in new shell growth at the outer lip, which exhibited the *P. pupa* color pattern. A clear line existed between the end of the *P. tristis* pattern and the beginning of the *P. pupa* pattern. *P. pupa* moved into the brackish pool showed immediate pattern switches in their new growth. New shell growth was black with white spots, in contrast to the rest of the shell, which was white with black lines. In the second experiment, all *P. pupa* from 400 m away exhibited phenotypic changes similar to those in the first experiment (Fig. 1F). New shell growth at the outer lip exhibited the *P. tristis* color pattern while the rest of the shell exhibited the *P. pupa* color pattern. Color pattern change was more dramatic in these *P. pupa*, because they grew for a longer period before collection. As with the other transplant experiments, observed pattern changes were clear and abrupt.

Radulae taken from both *Puperita pupa* and *P. tris-*

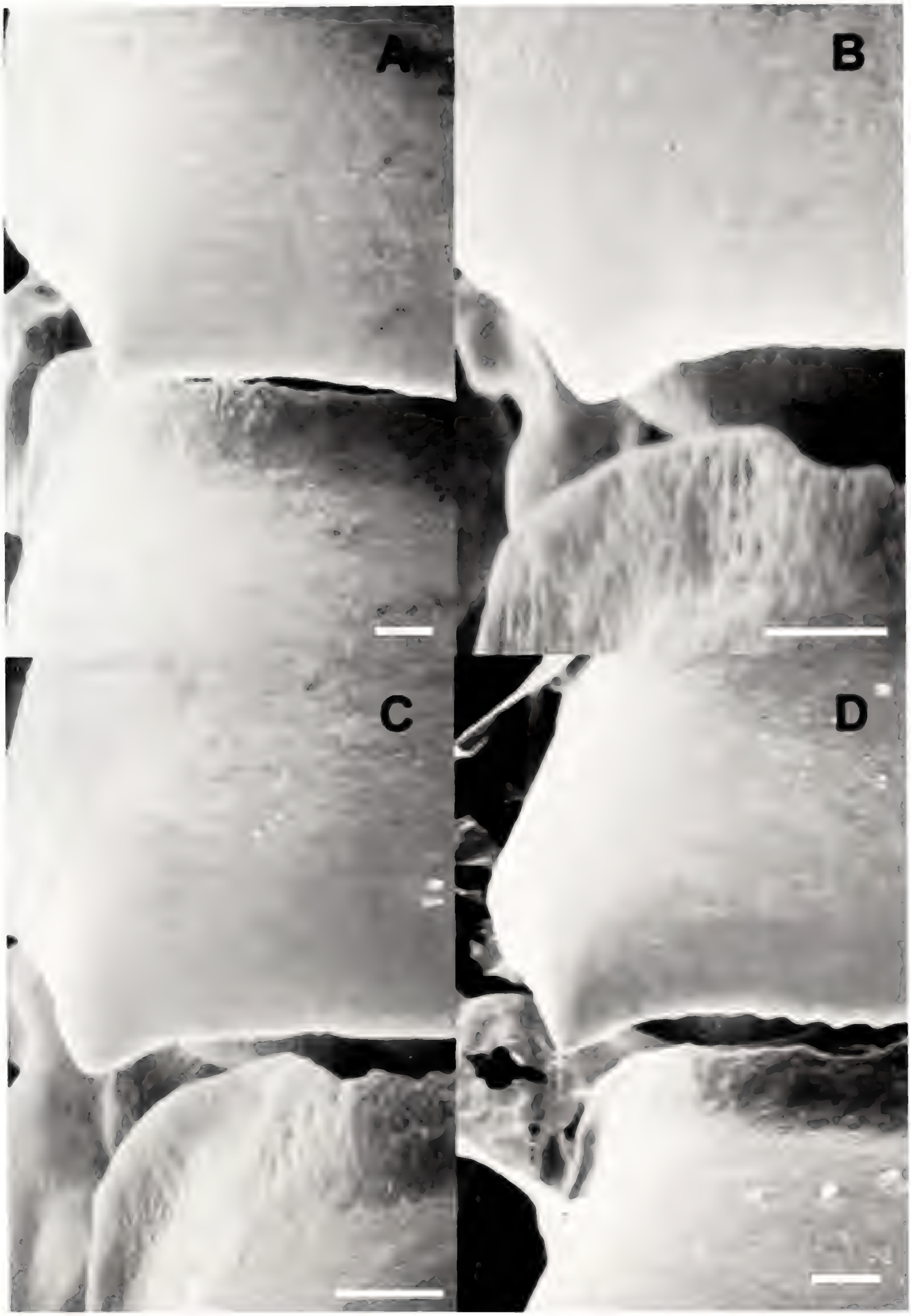

Fig. 2. E-lateral radula tooth showing cusp. A. *P. pupa*. B. *P. tristis*. C. Translocated *P. pupa* from nine month study. D. *P. pupa* from Ohio Key, Florida. Scale bar = 10 μm.

Table 2. Comparison of RAPD banding for the four DNA sets. Values below the diagonal are (number of unshared bands / total bands), and values above the diagonal are the average percent difference (APD).

LOT	Jamaica *P. pupa*	*P. tristis*	*N. virginea*	Florida *P. pupa*
Jamaica *P. pupa*	x	52.3	59.9	42.3
P. tristis	1041 / 1992	x	79.6	48.9
N. virginea	1381 / 2306	1578 / 1983	x	72.2
Florida *P. pupa*	738 / 1744	884 / 1808	1336 / 1851	x

tis show similar cusping of E-lateral teeth (Fig. 2). Radulae taken from *P. pupa* after the nine-month translocation were similar to those from non-transplanted *P. pupa* and *P. tristis*.

Average percent differences (APDs) for Jamaican *Puperita pupa* and *P. tristis*, Floridian *P. pupa* and Jamaican *Neritina virginea* individuals are summarized in Table 2. These figures represent all individual comparisons within each of the four groups. APDs obtained through between-group comparisons are also summarized in Table 2. These represent all individuals from one group compared to all individuals from another. Intraspecific APDs for *P. pupa* and *P. tristis* were similar to APDs for interspecific comparisons. The Tukey matrix (Table 3) of pairwise comparisons showed no single APD among the three *Puperita* groups (intra- versus interspecific) to be significantly different ($0.569 < p < 1.00$). APDs for intergeneric comparsions of *Puperita* and *Neritina* were significantly different (Table 2; $p < 0.05$).

DISCUSSION

Data presented here indicate that *Puperita pupa* and *P. tristis* are the same species. This conclusion is based on no variation in shell morphology, “switching” of shell color pattern after reciprocal transplantations, lack of differences in radula morphology, and RAPD assessment. Statistical analyses indicated size differences between *P. pupa* and *P. tristis* to be significant; however, this difference was on the order of tenths of millimeters, approximately one-third as large as those seen by Russell (1941). Additionally, a principal component analysis indicated no difference in measures of shell shape and proportion. Size and shape differences in neritids may be due to wave exposure (Murty and Rao, 1978), population density (Underwood, 1976), predation (Chilton and Bull, 1984), or other factors.

The phenotype of each putative species was induced experimentally following reciprocal transplantation into different habitat types, similar to changes shown in other gastropods by Neumann (1959). Separation of the two putative species has been historically based on shell color and pattern (Abbott, 1974). Russell (1941) noted that the “...color *per se* of the individuals of the family Neritidae is of no value as a specific determinant... pattern of colors, however, is of far greater importance, since certain species possess a quite constant type of color application to the shells.” This does not appear to be the case with *Puperita pupa*, as we have shown that individuals can express both color patterns.

We suggest that *Puperita pupa* exhibits phenotypic variation in response to environmental salinity. We believe the *“pupa”* phenotype is indicative of a saline environment, while the *“tristis”* phenotype indicates a brackish environment. However salinity was the only factor measured in our experiments, and, as cited previously, other environmental factors have been shown to influence gastropod phenotypes. If salinity is a major factor it might explain Russell’s (1941) observation that the ranges of both species overlap, but that they do not extensively coexist within a given area. In an environment composed of saline and brackish pools, similar to that seen at Urchin Cove, it is plausible that salinity-driven phenotypes of a single species would not be syntopic.

Plasticity in radulae has been documented (Padilla, 1998; Simison and Lindberg, 1999) though we

Table 3. Tukey matrix of pairwise comparisons probabilities. Significant differences ($p < 0.05$) are highlighted in bold. PP: *Puperita pupa*, PT: *P. tristis*, NV: *Neritina virginea*, all from Jamaica. FP: *P. pupa* from Florida.

Comparison	PP:PT	PP:NV	PT:NV	PP:FP	PT:FP	FP:NV
PP:PT	1.000					
PP:NV	0.758	1.000				
PT:NV	**0.000**	**0.001**	1.000			
PP:FP	0.569	0.051	**0.000**	1.000		
PT:FP	0.997	0.471	**0.000**	0.839	1.000	
FP:NV	**0.003**	0.083	0.533	**0.000**	**0.001**	1.000

show little evidence of plasticity in *Puperita pupa*. Baker (1923) noted that cusping of the E-lateral tooth is variable, and that cusp number may be age dependent. Roger (1934) found that cusping may vary within a small area of the specimen. Russell (1941) suggested that the radula is changeable and not an infallible character, and should be used in conjunction with others to diagnose identity. We do not believe Russell's observations on tooth cusping in *Puperita* to be species diagnostic, though we did not specifically test for environmental effects on radula morphology.

The RAPD technique indicated the two putative species exhibit low levels of genetic differentiation. Statistical treatments of the average percent differences showed no significant differences between the two nominal *Puperita* species. The Tukey test applied to average percent differences showed no significant difference between intraspecific and interspecific differentiation. This suggests that individuals of both species, regardless of geographic location or presumed species identity, can not be separated from each other. Russell (1941) argued that *Puperita pupa* should be placed either in *Neritina* or kept separate, and suggested keeping *Puperita* apart because it did not entirely exhibit characteristics of *Nerita* or *Neritina*. The RAPD markers showed a distinction between *P. pupa* and *Neritina virginea*, and support their standing as separate species. Whether *P. pupa* belongs in the genus *Neritina* remains to be seen. RAPD markers have been useful in assessing relationships in a variety of unrelated taxa (Chapco *et al.*, 1992; Crossland *et al.*, 1993; Shi *et al.*, 1996) with results concordant with other methods used to assess genetic relatedness (Guirao *et al.*, 1995; Comincini *et al.*, 1996; Szmidt *et al.*, 1996). We believe that RAPD analysis supports the existence of a single *Puperita* species, and offers evidence that *P. pupa* and *N. virginea* are separate taxa.

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Embryonic stages and feeding substances of the South American volutid *Voluta musica* (Caenogastropoda) during intracapsular development

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Abstract: South American volutids are very homogeneous regarding their reproductive patterns. They generally spawn egg capsules with few eggs, the embryos feed on substances contained in the intracapsular fluid, and they hatch as crawling juveniles. *Voluta musica* inhabits soft bottoms between 1 and 2 m depth at Isla Caribe, eastern coast of Venezuela. The spawn consists of a single egg capsule with one to five eggs embedded in a dense, mucous liquid, each egg measuring about 330 µm in diameter. The egg capsules have an internal volume that varies from 500 to 1500 µl. At hatching, between 10 and 310 µl of liquefied fluid remain inside the egg capsule, the rest of the capsule is filled with the crawling juveniles, which measure approximately 7 mm in shell length. The protein and sugar content of the embryos and intracapsular liquid were measured during different stages of development in order to determine the amount of food available for the embryo during early development, and if such contents were enough to account for the totals found in the hatchlings. At the first stage (uncleaved egg stage), the total protein content of the intracapsular liquid varies between 30 and 90 mg among different capsules, including the negligible amount of about 20 µg contained by the four eggs. At hatching, up to 480 µg of protein remain in the intracapsular liquid and the hatchlings contain about 8 mg of protein each. The intracapsular veliger stage is the most important feeding stage and is characterized by a very large velum, a small foot and a non-calcified shell. The total sugar content of the intracapsular liquid at the first stage varies between 3000 and 5000 µg, including less than 40 µg of sugar contained by the four eggs. At hatching, the capsule liquid contains about 100 µg of sugar and each juvenile contains about 1400 µg of sugar. Results indicate that the embryos feed on the intracapsular liquid, the increase in their protein and sugar content being due to the uptake of these substances, which are contained in enough quantity in the intracapsular liquid to account for the amount found in hatchlings. A comparison of the total protein available in the intracapsular liquid and nurse eggs of different species with extraembryonic food sources is given.

Key Words: embryonic development, protein, sugar, Volutidae, hatching size, intracapsular liquid

The tropical volutid *Voluta musica* Linnaeus, 1758 is commonly found in shallow waters of the southern Caribbean, living on mud or sandy bottoms and in *Thalassia testudinum* König, 1805 beds (Flores, 1978). This caenogastropod is distributed from the Greater Antilles to Surinam including the Netherlands Antilles, West Indies and British Guyana (Clench and Turner, 1970; Abbott, 1974). On the Caribbean coast of Venezuela, this species has been reported between the Paraguaná Peninsula (Falcón State) to the west, and Puerto La Cruz (Sucre State) to the east (Coomans, 1958: Gibson-Smith, 1973). It has also been reported at the islands of La Orchila, Los Testigos (Clench and Turner, 1964), Archipiélago de Las Aves (Flores, 1978) and Archipiélago de Los Roques (Work, 1969; Gibson-Smith, 1973).

Clench and Turner (1970), Gibson-Smith (1973), Von Cosel (1976) and Flores (1978) described the spawn and juveniles of *Voluta musica*. The egg capsules are found attached to hard substrata, usually to the internal side of empty bivalve shells. The egg capsules are hemispheric and measure approximately 18 mm in basal diameter. Gibson-Smith (1973) reported three or four embryos inside each egg capsule, all of them developing to the hatching stage.

A summary of the reproductive patterns found in the Volutidae is given by Penchaszadeh *et al.* (1999).The first mode consists of large solitary capsules resting freely on the sea bottom or attached to a hard substrate. This pattern is found in all American volutids up to now studied: *Adelomelon brasiliana* (Lamarck, 1811), *Odontocymbiola magellanica* (Gmelin, 1901), *Zidona dufresnei* (Donovan, 1823), *A. ancilla* (Lightfoot, 1786), *A. beckii* (Broderip, 1836) (Penchaszadeh *et al.*, 1999), *Voluta virescens* Lightfoot, 1786 (Bandel, 1976); *Harpovoluta charcoti* (Lamy, 1910) (Hain, 1992). The second pattern, found in West African volutids consists of the incubation of the egg capsule in a pedal gland: genus *Cymbium* Röding, 1798 (Marche-Marchad, 1968, 1980). The third pattern consists of a composite egg mass with numerous capsules and is typical of volutids of the Indo-Pacific and Australian regions: *Melo miltonis* (Griffith and Pidgeon, 1834) (Knudsen, 1993), *M. melo* (Lightfoot, 1786) (Amio, 1963). All three patterns result in a small number of large embryos having direct development. Reported extraembryonic food sources are nurse eggs in the genus *Cymbium* (Marche-Marchad, 1968, 1980) and in *V. virescens* (Bandel, 1976) or the intracapsular fluid of the internal layer of the egg capsule (De Mahieu *et al.*, 1974; Penchaszadeh *et al.*, 1999). In the Indo-Pacific species, no extraembryonic food source has been reported.

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The encapsulation of eggs within structures such as egg capsules is a widespread phenomenon among caenogastropods. The egg capsules may provide protection against predation and physical stress, against bacterial attack (because the capsule fluid is axenic in some species, Lord, 1986) and also, they may contain extraembryonic feeding substances such as nurse eggs, proteins and other substances in the capsule fluid and capsule wall material (Miloslavich, 1996a; Pechenik, 1986; Rawlings, 1994). Studies of the biochemical composition of the intracapsular liquid of several caenogastropod species have been carried out: *Adelomelon brasiliana* (De Mahieu *et al.*, 1974), *Busycon carica* (Gmelin, 1791) and *B. canaliculatum* (Linnaeus, 1758) (Harasewych, 1978), *Nucella lapillus* (Linnaeus, 1758) (Stockmann-Bosbach and Althoff, 1989) and *Prunum prunum* (Gmelin, 1791) (Penchaszadeh and Rincón, 1996). Such studies indicate that the intracapsular fluid of these species is composed of proteins and carbohydrates that decrease in concentration throughout development.

In this study, the intracapsular development of *Voluta musica* from the egg to the hatching stage is described. Protein and sugar content of the embryos and the intracapsular liquid is measured in order to determine: (1) the amount of food available for the embryo during early development, (2) ingestion stages, (3) the concentration of these substances throughout development and (4) if the intracapsular liquid contains enough protein and sugar to account for the amount found in the hatchlings.

MATERIALS AND METHODS

Specimens

Egg capsules were collected in April 1994 at Isla Caribe, Chacopata, northern Araya Peninsula, Estado Sucre, Venezuela (10°42`11" N, 63°52`57" W), between 1 and 2 m depth on soft bottoms (sand, mud and *Thalassia testudinum* beds). Egg capsules were usually found attached to the internal side of empty bivalve shells of the genera *Atrina* Gray, 1842, *Pinna* Linnaeus, 1758 and *Trachycardium* Mörch, 1853. A total of 230 egg capsules were collected. Some of the egg capsules were preserved in 5% formalin and some were kept in aquaria at a temperature of 25-27°C in aerated, non-circulating seawater.

Development

The following aspects of the spawn were studied: size of egg capsules, number and size of eggs and developing embryos within egg capsules, observations of the different stages of development and the number of whorls of the embryonic shell. Observations were carried out with fresh and preserved material.

Biochemical Procedures

The egg capsule content consisted of two fractions: embryos and intracapsular liquid. The volume of the intracapsular liquid was measured by extracting it from the capsule with a 20 µl Pipetmann micropipet (precision ± 1 µl). A previous analysis of the eggs was carried out in order to determine their amount of protein and sugar. The eggs were carefully separated from the intracapsular fluid and their protein and sugar content was measured. The protein content varied between 4 and 5 µg per egg and the sugar content was less than 10 µg per egg. These values are overestimated because some of the intracapsular fluid was inevitably still attached to the eggs. For further determinations, embryos at very early stages of development were not separated from the intracapsular liquid because they were embedded in it and separation was difficult without causing harm. Embryos were successfully separated from the liquid once they reached the veliger stage. The material was flash-frozen while fresh in 1.5 ml eppendorfs at -4°C and once frozen, were kept at -70°C for protein and sugar determinations.

Protein was determined following the Bio-Rad protein assay procedure based on the Bradford method (Bradford, 1976). Bovine serum albumin (BSA) was used as a standard. Samples were left overnight in 0.5 N NaOH and thoroughly homogenized.

Total sugar was determined by a modification of the Herbert *et al.* (1971) phenol method. Samples were left overnight and homogenized in citrate buffer (0.1 M, pH 5.0), 50 µl of phenol (80%) were added, mixed with a vortex and incubated at room temperature for 40 minutes. After incubation, 5 ml of concentrated sulfuric acid were added with a fast-flowing pipette and carefully shaken. Readings were taken at 480 nm after the samples were cooled to room temperature (between 22 and 25°C). Analytical saccharose was used as a standard.

RESULTS

Development

The egg capsules of *Voluta musica* were hemispheric, lenticular shaped and attached to the substrate by the flat side. The convex surface was smooth and it had a preformed exit plug consisting of a suture line on one side of the capsule. The external membrane was thick and resistant. The mean basal diameter of the egg capsule was 18.8 ± 1.9 mm (n = 27, range 15-23 mm) and the mean height was 8.6 ± 0.9 mm (n = 27, range 6-10 mm). The intracapsular fluid was transparent, with a gelatinous consistency at the early stages of development and a liquid consistency at the final stages.

Each egg capsule contained between one and five eggs (3.6 ± 0.9, mean ± st. dev., n = 145), all of which developed to the hatching stage. The eggs were pinkish yellow and measured approximately 330 µm in diameter (334 ± 36 µm, n = 56). The first two cleavages produced two and four macromeres respectively, all of equal size. In the third cleavage, each macromere gave rise to a small micromere at the animal pole (Stage 1), this embryo measured about 340 µm in diameter. After gastrulation, the embryo had two distinct regions, a yellow region corresponding to yolk and a pink-orange region corresponding to the visceral mass. The organic matrix of the shell was observed as a transparent grainy layer at the vegetal pole. At the animal pole, the velar cone was observed as well as an incipient velum (Stage 2). This embryo measured approximately 450 µm in length. The early veliger (Stage 3) measured approximately 510 µm lengthwise, it had a small velum (400 µm), and the organic matrix of the shell and the body was pinkish yellow. The second veliger (Stage 4) was characterized by a bilobed velum that was more than 3 mm wide; the shell was very fragile and torsion had begun; this veliger measured about 1200 µm in length. The third veliger (Stage 5), measuring approximately 2300 µm lengthwise was characterized by a very large velum, which was more than 10 mm wide and 8 mm high. The shell was transparent and very fragile. Torsion was complete and a small foot was visible. The veliconch (Stage 6) measured about 4000 µm in shell length and was also characterized by a very large velum, densely ciliated, the cilia measuring between 18.8 and 47 µm. At this stage, calcification of the shell began, and the foot was still small. The pediveliger (Stage 7) measured around 4500 µm in shell length and was characterized by a calcified shell, a large foot and an almost entirely resorbed velum. None of the previous stages survived more than a few hours when excapsulated in sea water. The prehatching stage (Stage 8) measured about 4700 µm; it had a well developed crawling foot, the velum was completely absent, and the shell was pigmented with black spots on an orange background. At the hatching stage (Stage 9), the shell measured about 7100 µm in length; it was orange and had the typical pentagram pattern of the species. The foot and siphon were pigmented with pink spots (Table 1, Figs. 1 and 2).

Biochemical content of embryos and intracapsular fluid

During development, the volume of the intracapsular liquid decreased almost 10 times (Table 2). Between the egg stage and the hatching stage, the total protein content of the intracapsular liquid decreased more than 120 times while the sugar content decreased about 50 times. The protein concentration also decreased three times and the sugar concentration decreased six times (Table 2). The most significant decrease occurred at the third veliger stage (Stage 5) when the velum reached its maximum size.

The protein content of the embryos increased more than 1600 fold from the egg stage to hatching, while the sugar content increased nearly 50 fold to the prehatching stage and then decreased to the hatching stage down to 34 fold in relation to the egg stage (Table 3, Fig. 3). The most significant increases in content occurred from the egg stage to the early veliger stage (70 fold in protein content) and between the third veliger to the veliconch stage (almost 10 fold in protein content and three fold in sugar content). These increases are coincident with foot development and shell calcification. Protein and sugar analysis of the intracapsular liquid at the first and last stages of development indicate that there is enough of these substances in the intracapsular liquid to account for the total found in the hatchlings (Table 4).

DISCUSSION

Development

As a general rule, the South American volutids are very homogeneous regarding their reproductive patterns. Commonly, the egg capsules are attached to hard substrates; the fact that *Adelomelon brasiliana* spawns free egg capsules is a remarkable adaptation to shallow sandy bottoms given that they may be carried away by the currents but never buried in the sand (Penchaszadeh and De Mahieu, 1976). With the exception of *Voluta virescens*, which according to Bandel (1976) spawns egg capsules containing about 200 eggs of which the one or two that develop ingest the rest as nurse eggs, the South American species spawn egg capsules with few eggs; the embryos feed on substances contained in the intracapsular fluid; development is direct (intracapsular metamorphosis); and hatchlings may have a shell length of more than 10 mm (Carcelles, 1944; de Mahieu *et al.*, 1974; Penchaszadeh and De Mahieu, 1976; Penchaszadeh, 1988; Hain, 1992; Penchaszadeh *et al.*, 1999).

The volutids of the West African, Indo Pacific and Australian regions present different reproductive patterns. West African volutids incubate the egg capsule in the pedal gland for a period of up to five months. In the genus

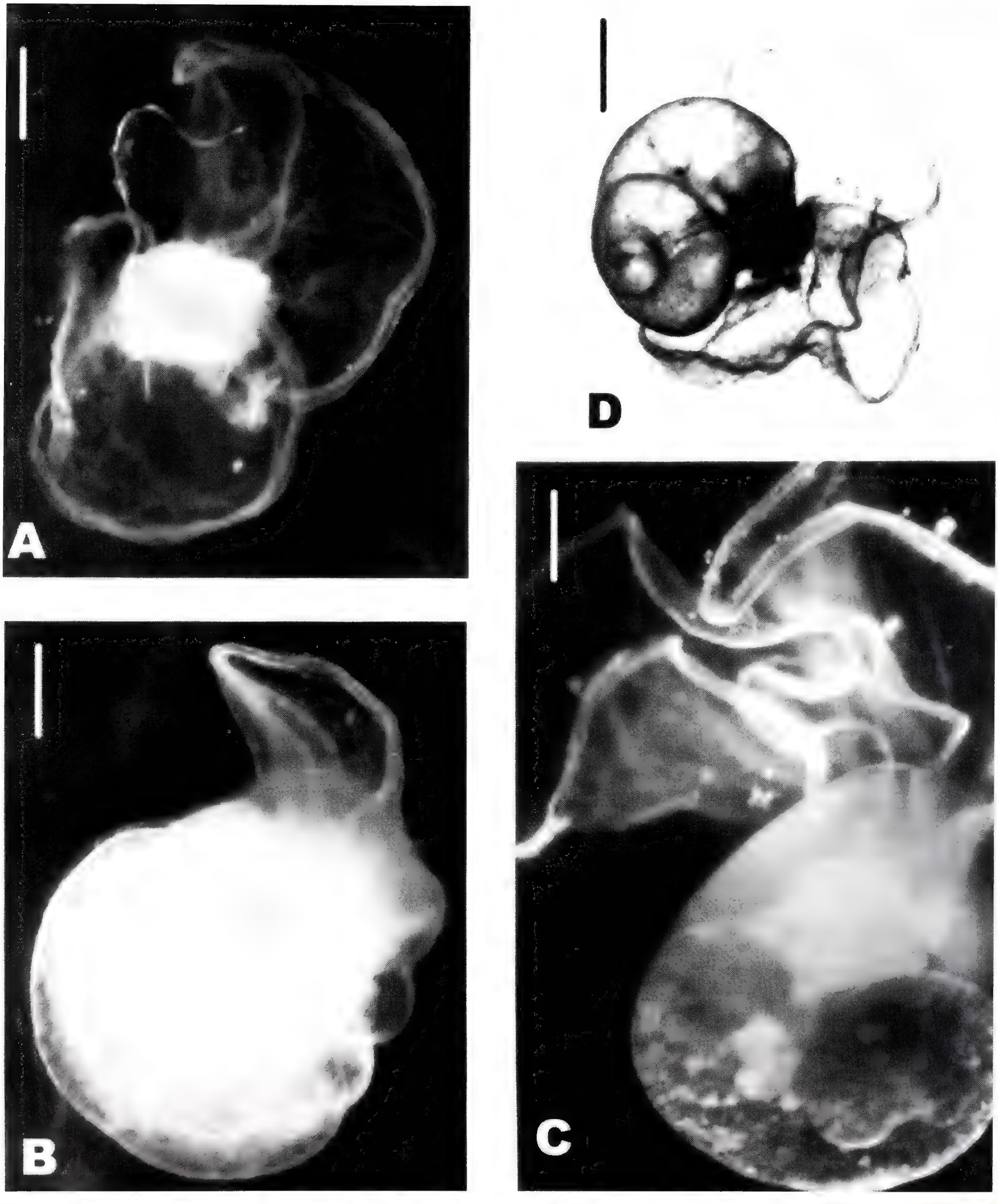

Figure 1. Intracapsular veliger stages of *Voluta musica.* **A.** First veliger, scale bar: 120 µm. **B.** Second veliger, scale bar: 280 µm. **C.** Third veliger, scale bar: 500 µm. **D.** Veliconch, scale bar: 1500 µm.

Table 1. Summary of the intracapsular development of *Voluta musica*. For embryo size, values indicate mean ± standard deviation; numbers in parenthesis indicate range.

STAGE	Size of embryos (μm)	Number of volutions	Remarks
0 Egg	339.3 ± 36.4 (250 - 450) n = 56		Yellow - pinkish uncleaved eggs
1 2, 4, 8 cells	340.2 ± 29.8 (288 - 384) n = 18		Early segmentation, first 3 cleavages
2 Embryo	442.9 ± 50.3 (360 - 550) n = 21		Gastrulation Organic matrix of the shell starts Origin of the velar cone Incipient velum Posterior yellow region with yolk Anterior pink region with visceral mass
3 First veliger	511.4 ± 126.8 (332 - 780) n = 58		Small velum (400 μm wide) Organic matrix of shell Body is yellow-pinkish
4 Second veliger	1163.8 ± 206.3 (860 - 1620) n = 21	< 1	Development of the velum (bilobed, > 3 mm wide) Very fragile shell Torsion begins
5 Third veliger	2285.5 ± 816.5 (1120 - 4160) n = 43	1 - 2	Very large velum (> 10 mm wide and > 8 mm high) Fragile shell Torsion completed Small foot
6 Veliconch	3939.6 ± 880.4 (1680 - 5610) n = 95	1 - 2+338°	Very large velum Calcification of shell begins (still transparent) Small foot
7 Pediveliger	4490.3 ± 272.1 (3960 - 4950) n = 15	3 - 3+158°	Velum absorption Calcified shell Large foot
8 Prehatching	4712.0 ± 678.1 (3280 - 5920) n = 40	3+45° - 3+348°	Velum absent Shell shows pigmentation (black spots on orange background) Well developed crawling foot
9 Hatching	7173.6 ± 610.6 (6400 - 8640) n = 22	4	Orange shell with pentagram pattern Pigmented foot and siphon (pink spots)

Cymbium, there are two extraembryonic food sources, nurse eggs (several thousand) and substances contained in the intracapsular fluid (Marche-Marchad, 1968, 1980). Hatching takes place as a veliconch, which measures up to 50 mm in shell length.

The *Melo* species from the Indo Pacific, southern Japan and Australia present a composite egg mass, in a pineapple or cylindrical shape, the number of egg capsules is variable and they are arranged in a spiral. Only one embryo per capsule develops and hatches as a crawling juvenile (Tokioka, 1962; Amio, 1963; Knudsen, 1993). No nurse eggs have been reported, however, the intracapsular liquid may contain proteins given the observations provided by Knudsen (1993), who described that the intracapsular liquid of capsules with embryos almost ready to hatch was a clear fluid that was transformed into a filamentous mass some time after preservation in 10% formalin.

An outstanding characteristic during the embryonic development of *Voluta musica* is the presence of a large velum. According to Giese and Pearse (1977), "prosobranchs" with direct development usually have a small velum. The velum could have several functions in species

Table 2. Total protein and sugar in the intracapsular liquid of *Voluta musica*. Values indicate mean ± standard deviation; numbers in parentheses indicate range.

STAGE	VOLUME OF INTRACAPSULAR LIQUID (µl)	TOTAL PROTEIN (mg)	µg PROTEIN / µl	TOTAL SUGAR (mg)	µg SUGAR / µl
Egg (Stage 0)	879.4 ± 270.8 n = 18 (400 - 1500)	57.1 ± 18.0 n = 9 (28.5 - 89.5)	69.5 ± 14.5 n = 9 (49.7 - 88.6)	4.9 ± 0.8 n = 9 (3.9 - 6.4)	6.0 ± 2.8 n = 9 (2.9 - 10.0)
Early Veliger (Stage 3)	861.2 ± 239.5 n = 26 (450 - 1400)	41.1 ± 13.6 n = 8 (13.3 - 54.4)	53.3 ± 15.6 n = 8 (27.2 - 73.1)	5.4 ± 1.4 n = 18 (2.6 - 7.5)	6.1 ± 1.3 n = 18 (3.7 - 8.5)
Third Veliger (Stage 5)	493.8 ± 182.3 n = 16 (150 - 750)	13.4 ± 5.0 n = 11 (7.8 - 25.4)	33.9 ± 13.3 n = 11 (15.6 - 56.8)	3.4 ± 2.0 n = 5 (1.6 - 6.4)	5.4 ± 2.2 n = 5 (2.7 - 8.6)
Veliconch (Stage 6)	307.4 ± 145.4 n = 19 (50 - 715)	9.6 ± 4.0 n = 8 (3.3 - 17.4)	26.2 ± 10.7 n = 8 (5.1 - 40.9)	1.1 ± 0.4 n = 9 (0.4 - 1.5)	5.2 ± 2.2 n = 9 (2.9 - 10.0)
Prehatching (Stage 8)	285.7 ± 171.4 n = 7 (130 - 600)	5.2 ± 3.0 n = 5 (2.1 - 9.0)	22.5 ± 11.2 n = 5 (5.1 - 32.6)	0.9 ± 0.3 n = 2 (0.7 - 1.2)	3.6 ± 2.3 n = 2 (1.9 - 5.2)
Hatching (Stage 9)	94.0 ± 127.4 n = 5 (10 - 310)	0.45 ± 0.04 n = 2 (0.42 - 0.48)	22.5 ± 1.9 n = 2 (21.2 - 23.9)	0.1 ± 0.1 n = 3 (0.008 - 0.3)	0.9 ± 0.1 n = 3 (0.8 - 0.9)

with intracapsular metamorphosis, the first is for handling and ingesting nurse eggs (Fioroni, 1967; Hadfield and Iaea, 1989) and the second is for respiration through gelatinous egg masses (Hunter and Vogel, 1986). The velum of *V. musica* is densely ciliated and characterized by small cilia. According to Hadfield and Iaea (1989), the velum of the vermetid *Petaloconchus montereyensis* Dall, 1919 is highly modified for the ingestion of nurse eggs during intracapsular development, lacking the necessary structures for swimming and feeding during planktotrophic life (pre- and post-oral ciliary bands and food groove). Excapsulated veligers of *V. musica* are also unable to swim, and the large velum is probably used either for feeding (which occurs mostly at this stage of development) or for respiration. Resorbtion of the velum begins at the pediveliger stage (Stage 7), when more than 80% of the protein and sugar content has been consumed from the intracapsular liquid. Hadfield and Iaea (1989) proposed that velar resorbtion is nutritionally triggered, that is, it occurs in response to the absence of an external food supply, which in this case, could be the low contents of protein and sugar within the egg capsule fluid.

Biochemical content of the embryos and intracapsular liquid

Gastropod egg capsules are very complex structures; the microstructure is composed of three or four layers (D'Asaro, 1988; Rawlings, 1990, 1994; Tamarin and

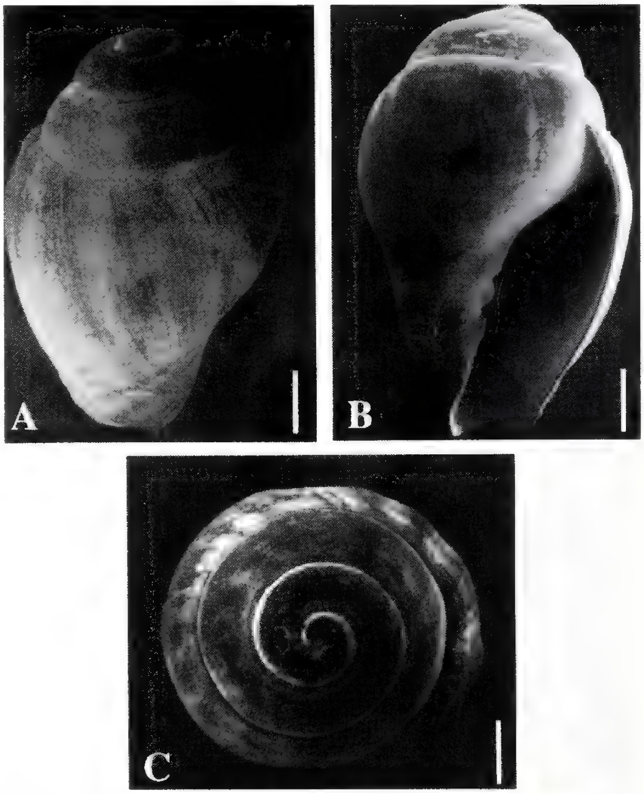

Fig. 2. SEM of the hatching shell of *Voluta musica*. **A.** Dorsal view. **B.** Aperture. **C.** Spire. Scale bar: 1 mm.

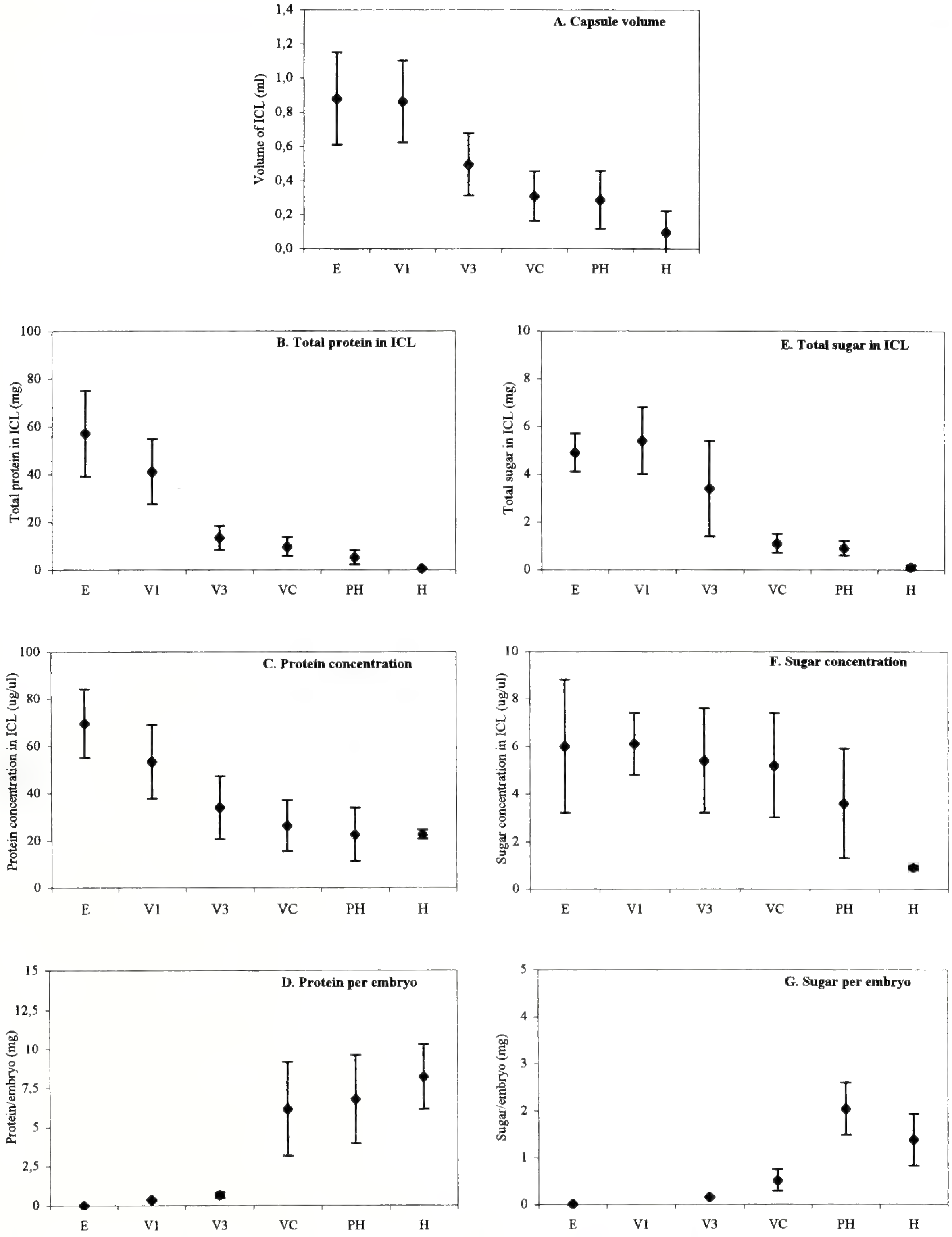

Figure 3. Protein and sugar in the intracapsular liquid (ICL) and in embryos of *Voluta musica* at different stages during intracapsular development. **A.** Volume of intracapsular liquid. **B.** Total protein in the intracapsular liquid. **C.** Protein concentration in the intracapsular liquid. **D.** Total protein per embryo. **E.** Total sugar in the intracapsular liquid. **F.** Sugar concentration in the intracapsular liquid. **G.** Total sugar per embryo. Error bars are standard deviation. Abbreviations: E: egg (stage 0), V1: First veliger (stage 3), V3: third veliger (stage 5), VC: veliconch (stage 6), PH: prehatching (stage 8), H: hatching (stage 9).

Table 3. Total protein and sugar content per embryo at different stages of development of *Voluta musica*. Values indicate mean ± standard deviation; numbers in parenthesis indicate range.

STAGE	µg protein / embryo	µg sugar / embryo
Egg (Stage 0)	Less than 5 µg / egg	Less than 40 µg / egg
Early veliger (Stage 3)	354.5 ± 26.2 n = 2 (335.9 - 373.0)	----------
Third veliger (Stage 5)	641.9 ± 176.3 n = 5 (352.0 - 803.0)	151.2 ± 5.1 n = 2 (147.6 - 154.8)
Veliconch (Stage 6)	6164.2 ± 3019.8 n = 21 (1173.0 - 10357.2)	505.7 ± 230.2 n = 11 (193.1 - 816.9)
Prehatching (Stage 8)	6777.8 ± 2836.5 n = 10 (1992.0 - 11583.0)	2031.3 ± 560.3 n = 7 (1147.8 - 2653.9)
Hatching (Stage 9)	8213.1 ± 2071.7 n = 9 (4521.6 - 11719.2)	1371.9 ± 556.7 n = 8 (603.3 - 2349.5)

Carriker, 1967) and they are biochemically composed of proteins, amino acids, carbohydrates, acid mucopolysaccharides, COOH groups and lipids (Hunt, 1966; Miloslavich, 1996b, Sullivan and Maugel, 1984). There are very few studies that test the permeability of the capsule wall to different substances. Pechenik (1982) reported that the capsule walls of three muricid species are permeable to water, salts and to small carbohydrate molecules (glucose) and Hawkins and Hutchinson (1988), reported that the egg capsules of the muricid *Ocenebra erinacea* (Linnaeus, 1758) are permeable to water and salts at all stages of development. Moreover, Pechenik (1983), reported that the egg capsules of another muricid species are permeable to NaCl and water, but substantially less permeable to small organic molecules such as amino acids, glucose and sucrose, and that the existing solute molecules are inorganic ions. These studies seem to indicate that substances such as proteins and other large molecules remain in the egg capsule throughout development and therefore can be used by the embryos as a nutrition source.

During the intracapsular development of *Voluta musica*, protein and sugar are incorporated mostly between the third veliger (Stage 5) and veliconch (Stage 6) stages, when there is a marked decrease in the total content of these substances in the intracapsular liquid, and the embryos show a marked increase of both protein and sugar. At these stages, the velum of the embryos is very large and shell calcification and foot development begin. De Mahieu *et al.* (1974) reported that the embryos of *Adelomelon brasiliana* also incorporate most of the protein from the intracapsular liquid during shell calcification. Penchaszadeh and Rincón (1996) have found similar results in *Prunum prunum*. As pointed out by Wilbur (1972), shell formation integrates a series of physiological, biochemical and crystallization processes, which result in a highly organized structure of calcium carbonate crystals in an organic matrix (composed mainly of proteins, free amino acids and mucopolysaccharides, Grégoire, 1972).

The uncleaved egg size of *Voluta musica* (250 to 450 µm) is the largest recorded yet among the South American volutids, comparable only to that of *Odontocymbiola magellanica,* which measures between 280 and 300 µm (Penchaszadeh and De Mahieu, 1976). The importance of egg size and the amount of extraembryonic food sources during development has been discussed by several authors (Fioroni,1982). Fioroni (1988) has

Table 4. Biochemical (protein and sugar) balance between the egg and hatching stage of *Voluta musica*. Values at the hatching stage were calculated for a mean number of four (4) developing embryos per capsule.

	TOTAL IN EGG CAPSULE AT EGG STAGE (mg) (eggs + liquid)	TOTAL IN 4 EMBRYOS AT HATCHING (mg)	TOTAL IN LIQUID AT HATCHING STAGE (mg)	TOTAL IN EGG CAPSULE AT HATCHING STAGE (mg) (embryos + liquid)	BALANCE
PROTEIN	60 (*)	32.8	0.45	32.8 + 0.45 = 33.25	Positive
SUGAR	5 (**)	5.6	0.10	5.6 + 0.1 = 5.7	± Equal
TOTAL (Protein + sugar)	65	38.4	0.55	38.4 + 0.55 = 38.95	Positive

(*) Includes 20 µg of protein contained by the four eggs.
(**) Includes 40 µg of sugar contained by the four eggs.

Table 5. Comparison of the total protein available in the intracapsular liquid (ICL) and nurse eggs (NE) of different species with extraembryonic food sources at the first stage of development (uncleaved egg).

PROTEIN AVAILABLE PER EMBRYO IN SPECIES THAT FEED ON THE INTRACAPSULAR LIQUID:

SPECIES (Family)	Total protein in ICL	Total volume of ICL	Protein concentration in ICL	Mean number of embryos	Protein available per embryo (µg)	Hatching mode	Reference
Nucella lapillus (Muricidae)	0.23 mg	31.6 ± 8.9 µl	7.4 mg/ml (gastrula stage)	34 + 966 NE	220 + 30 NE each	Crawling	Stockmann-Bosbach and Althoff, 1989
Urosalpinx cinerea (Muricidae)	"albumen"	5.4-19.8 µl	Not determined	1-19 8.12 ± 3.0	2 µl of albumen	Crawling	Rivest, 1986
Engoniophos unicinctus (Buccinidae)	100-150 µg	10 µl	12.5 mg/ml	4-5	30	Crawling + velar remains	Miloslavich and Penchaszadeh, 1994 Miloslavich, 1999
Busycon carica (Melongenidae)	1.9 mg	500 µl	3.8 mg/ml	55	30	Crawling	Harasewych, 1978 Conklin, 1907
Busycon canaliculatum (Melongenidae)	4.35 mg	500 µl	8.7 mg/ml	110	40	Crawling	Harasewych, 1978
Prunum prunum (Marginellidae)	0.14-0.26 mg	6-11 µl	23.4 ± 6.4 mg/ml	1	200	Crawling	Penchaszadeh and Rincón, 1996
Adelomelon brasiliana (Volutidae)	1.54 g	77 ml	20 mg/ml	22	70,000	Crawling	DeMahieu *et al.*, 1974 Penchaszadeh and DeMahieu, 1976
Voluta musica (Volutidae)	60 mg (*)	800 µl	69.5 ± 14.5 mg/ml	4	8,200	Crawling	Present work

(*) Includes 20 µg of protein contained by the four eggs.

PROTEIN AVAILABLE PER EMBRYO IN NURSE EGG FEEDING SPECIES:

SPECIES (Family)	Total protein in egg capsule content (Eggs + NE) (mg)	Ratio (NE: embryo)	µg of protein per egg	Protein available in NE for developing embryo (µg)	Hatching mode	Reference
Eualetes tulipa (Vermetidae)	0.54 (289 eggs)	1.5:1	1.9	2.85	Veliger	Miloslavich, 1996
Buccinum undatum (Buccinidae)	2.78 (918 eggs)	92:1	3.0	276	Crawling	Miloslavich, 1996
Buccinum cyaneum (Buccinidae)	1.25 (567 eggs)	189:1	2.2	415.8	Crawling	Miloslavich, 1996
Fasciolaria tulipa hollisteri (Fasciolariidae)	6.36 (3119 eggs)	446:1	2.0	892	Crawling	Miloslavich, 1996
Fusinus closter (Fasciolariidae)	0.66 (291 eggs)	17:1	2.3	39.1	Crawling + velar remains	Miloslavich, 1996

focused on species that complete development by ingesting nurse eggs and Miloslavich (1996a) has studied the biochemical value of the eggs and hatchlings of some nurse egg feeding species. The nourishing value of the intracapsular liquid was determined for a few caenogastropod species by De Mahieu *et al.* (1974), Harasewych (1978), Stockmann-Bosbach and Althoff (1989) and Penchaszadeh and Rincón (1996). The total protein available in the intracapsular liquid and nurse eggs of different species with extraembryonic food sources is summarized in Table 5.

This amount varies from 2.85 to 70,000 µg per embryo for *Eualetes tulipa* (Chenu, 1843) (Miloslavich, 1996a) and *Adelomelon brasiliana* (De Mahieu *et al.*, 1974) respectively. The hatching mode of *E. tulipa* (species with less than 3 µg available for each embryo) is as a veliger larva, while embryos from other species that ingested more than 30 µg of protein during intracapsular development hatch as crawling juveniles. The highest values are found in the Volutidae with 8,200 µg (*V. musica*) and 70,000 µg (*A. brasiliana*) of protein available per embryo.

The egg capsules found in the Volutidae are among the largest recorded for caenogastropods (Penchaszadeh *et al.*, 1999), and possibly contain more protein than other species. Other egg capsules comparable in size and morphology to those of Volutidae are found in some Buccinidae of the northern Pacific (subfamily Volutopsiinae). The egg capsules of the Volutopsiinae are very large (up to 66 mm in diameter), single laid and nearly hemispherical, an unusual morphology for Buccinidae. They are lined in the inside with a thick layer of albuminous substance on which the embryos feed after they have ingested the nurse eggs (very few). The size of the hatching embryos is very large, up to 20 mm in *Volutopsius norvegicus* (Gmelin, 1791) (Kantor, 1990). Gonor (1964) described two egg capsules of *Pyrolofusus deformis* (Reeve, 1847) from Alaska. These are globular, with a flat base firmly cemented to the substrate and measured 27 mm in diameter. One contained “a colorless, thick, jelly-like material in the basal portion and some soft yellowish material above this” and the other contained “three small snails which virtually filled the inside”. These observations indicate that the embryos probably consumed this thick material. A biochemical study of the intracapsular liquid of these egg capsules would be interesting to determine if not only the morphology but also the protein content is similar to volutids. In this way, more comparisons could be made about the diversity of maternal investment in the embryos of several species as well as how different families within the caenogastropods have resolved the problem of nutrition during intracapsular development.

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Habitat characteristics of Rocky Mountain (Colorado) populations of *Acroloxus coloradensis*

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Abstract: Six Colorado lakes that support *Acroloxus coloradensis* have significantly higher calcium concentrations and conductivity values than 28 lakes in Rocky Mountain National Park where *A. coloradensis* was not detected during intensive sampling. Calcium concentrations and conductivity also decrease significantly with increasing elevation. Low dissolved-ion concentrations may be a factor explaining the apparent absence of *A. coloradensis* in high-elevation lakes.

Key Words: *Acroloxus coloradensis*, calcium, capshell, Colorado, conductivity, Rocky Mountain National Park

Acroloxus coloradensis (Henderson, 1930), the Rocky Mountain capshell, has been described as "one of the rarest, unprotected mollusks" in the United States (Davis, G. M., unpublished letter to John Turner, Director, U. S. Fish and Wildlife Service, 27 Oct 1992; on file with U. S. Fish and Wildlife Service, Golden, Colorado). Only two populations were known to exist in the United States in 1992, when the U.S. Fish and Wildlife Service received a petition to list *A. coloradensis* as a federally endangered species: the type population in Peterson Lake, Colorado, (Walker, 1925; Bryce, 1970) appeared to be "nearly extirpated" (Clarke, 1993), while the population in Lost Lake, Montana, (Russell and Brunson, 1967) was potentially threatened by recreational use and traffic on an adjacent highway (Garza *et al.*, 1993). The request for endangered species protection prompted two groups to search for additional capshell populations during summer 1993. We sampled 20 lakes in Rocky Mountain National Park (north central Colorado, USA), and Pioneer Environmental Services sampled 27 lakes scattered throughout the Rocky Mountain region of Colorado (Pioneer Environmental Services, Inc., 1993). The 1993 surveys located four new capshell populations. We found *A. coloradensis* in Finch Lake on 5 Jul 1993, and Pioneer Environmental Services found populations in Teal (19 Jul 1993), Lost (20 Jul 1993), and Upper Big Creek (22 Jul 1993) Lakes. We sampled several additional lakes during the summers of 1994 and 1997 and found an *A. coloradensis* population in an unnamed pond in the Middle St. Vrain Creek drainage of Roosevelt National Forest, 4.9 km west of Peaceful Valley, Colorado, on 27 Jun 1997.

The recently discovered populations verify Bryce's (1970) prediction that "It is likely that living populations of *Acroloxus coloradensis* will be found to occur in other infrequent and scattered Rocky Mountain lakes...." More importantly, the new populations make it possible to further characterize the habitat requirements of *A. coloradensis*. This information will be valuable if a management plan or recovery plan is prepared for *A. coloradensis*.

METHODS

In order to check park lakes systematically for the presence of *Acroloxus coloradensis*, we divided Rocky Mountain National Park into six geographic sectors (Table 1) and sampled at least one-fifth of the lakes below 3400 m (≈ treeline) in each sector.

At each lake, we attempted to identify an area with wave-washed rocks on the downwind shoreline (Clarke, 1981) and sampled that site and three additional sites (if suitable rocky habitat was present) at approximately 90-degree intervals around the perimeter of the lake.

Most of the 1993 sampling was performed by three-person teams. At each sampling site, a dry-suited diver collected rocks from 0.6-1.2 meter and 1.2-1.8 meter depths and brought them to shore, where a second person examined the rocks for capshells. A third person collected and examined rocks from shallow (0-0.6 m) water. Each rock surface was visually examined and then scrubbed with a soft brush over Nitex 471-micron mesh to collect any dis-

Table 1. Geographic distribution of lakes sampled for *Acroloxus coloradensis* in Rocky Mountain National Park. Lists of lakes in each sector were compiled from destination tables in Dannen and Dannen (1985).

Sector	Number of lakes below 3350 m	Lakes sampled
East of Continental Divide		
North of 40.375°N	17	4
40.25°N to 40.375°	28	13
South of 40.25°N	18	8
West of Continental Divide		
North of 40.375°N	3	1
40.25°N to 40.375°N	8	2
South of 40.25°N	5	1
Totals	79	29

lodged organisms. Each site was sampled for approximately 30 minutes.

During 1994 and 1997, we altered our methods in four ways. We limited our sampling to 0-0.6 meter depths that could be accessed with hip boots because (1) park lakes do not exhibit the large water-level fluctuations (due to withdrawals for winter snow-making) that may account for the deep (~ 2 m) location of three capshells collected from Peterson Lake in 1992 (Clarke, 1993), (2) rocky substrata are often limited to the shallow periphery of park lakes (mucky substrata predominate in deep water), and (3) we had not previously found any molluscs in deep water that were not also present in shallow water. We eliminated the brushing of rock surfaces, since visual examination appeared to be an equally effective discovery method when capshells were present. We equalized our search effort by sampling 40 rocks at each station instead of searching for a standard amount of time. In four small lakes (< 0.5 ha) and in one medium-sized lake (~ 5 ha), we examined rocks along the entire rocky portion of the shoreline.

We determined the elevation of each lake from U.S. Geological Survey 1:24,000 topographic maps. In cases in which maps do not give lake surface elevations, we used the elevation of the first contour line below the lake.

We determined the surface area of each lake from U.S. Geological Survey 1:24,000 and 1:100,000 digital line graph files using Maptitude® geographic information system software (Caliper Corporation, Newton, Massachusetts). Drainage basin areas were estimated by sketching watershed divides on topographic maps and measuring the enclosed areas with a digitizing tablet or with the geographic information system software.

Because most of the Colorado capshell lakes have small watersheds with no natural, perennial inlet streams, we wondered if flushing rates are lower in capshell lakes than in non-capshell lakes. We estimated relative flushing rates by calculating the ratio between drainage basin area and lake surface area (flushing rate index = drainage basin area/ surface area).

Calcium concentrations were determined by flame atomic absorption spectrophotometry. We collected 500 mL water samples in acid-washed polyethylene bottles between 12 Jul and 1 Aug 1994. 2.5 mL of concentrated nitric acid were immediately added to each sample to suppress biological activity and to keep calcium in solution. The samples were prepared and analyzed according to EPA method 3005 (U. S. Environmental Protection Agency, 1994) during fall 1994 and winter 1995.

Conductivity measurements were collected between 10 Jul and 4 Aug 1997 with a Myron L model EP10 conductivity meter.

Surface geology was determined from the largest-scale U. S. Geological Survey geologic map available for each lake (Gable, 1969; Snyder, 1980; Braddock and Cole, 1990; Madole, 1991). Because the geologic maps use different map units (and because some map units are associated with a single lake), we grouped the surface geology map units into three categories (transported soils, metamorphic rock, and intrusive igneous rock) in order to have adequate sample sizes for statistical analysis. When a lake was bordered by more than one geologic map unit, we included the lake in each applicable category.

In order to monitor population densities with minimal disturbance of the natural rock substratum, we installed 40 artificial substrata (19.5 cm x 19.5 cm x 1.2 cm clay floor tiles) in Finch Lake during Jul 1994. The substrata are spaced at one-meter intervals in two transects running parallel to the shoreline, at water depths ranging from 18 to 80 cm. We have counted the number of capshells on the artificial substrata once a year (in late Jul or Aug).

During Jul, Aug, and Sep 1999, we measured temperatures in Finch Lake and the unnamed pond with Stowaway Tidbit temperature loggers (Onset Computer Corporation, Bourne, Massachusetts). The loggers were attached to the underside of artificial substrata (one logger in each lake) and were programmed to collect readings at hourly intervals.

RESULTS

The areas where we found *Acroloxus coloradensis* in Finch Lake and in the unnamed pond in Roosevelt National Forest closely match the description in Clarke (1981): *A. coloradensis* is concentrated in areas of wave-washed, silt-free rocks at the downwind end of each lake. Areas of maximum abundance occur where rocks are piled on top of each other. In both lakes, capshell abundance drops off sharply when individual rocks become separated by areas of mud or sand and in areas where rocks are covered by silt. There is abundant macrophytic vegetation (primarily *Sparganium minimum* [Hartman] and *Carex aquatilis* Wahlenberg) at the Finch Lake site and less-extensive coverage by the same two plant species at the "unnamed pond" site. We found *Gyraulus parvus* (Say, 1817) on rocks in both lakes. Fish are present in the unnamed pond but not in Finch Lake.

Table 2 identifies several differences between the six Colorado lakes that support capshell populations and 28 lakes in Rocky Mountain National Park that we have sampled intensively without finding *Acroloxus coloradensis*. The average elevation of the capshell lakes is significantly lower than the lakes without capshells. Seventeen of the 28 lakes without capshells are higher than Finch Lake, the highest lake with capshells. The capshell lakes have significantly higher calcium concentrations and conductivity values than the lakes without capshells. Due to large variations within both groups, the differences in mean surface area and mean flushing rate index are not statistically significant.

There are several significant patterns in the habitat data that could affect capshell distributions. Calcium concentrations and conductivity both decline with increasing elevation (Figs. 1 and 2). Calcium concentrations and conductivity are also strongly correlated (Fig 3). Calcium concentrations and conductivity are not significantly correlated with flushing rate, lake surface area, or watershed area (Table 3). Surface area (r = -0.29), watershed area (r = -0.33), and flushing rate (r = -0.24) do not vary significantly with elevation.

Three of the lakes we sampled (Lily, Peterson, and Poudre) are located adjacent to paved highways and have exceptionally high calcium and conductivity values (possibly due to de-icing salts, roadside dust, or vehicle emissions). Because these lakes act as outliers in regression and correlation analyses, we performed statistical analyses with and without the roadside lakes in order to minimize the possibility that anthropogenic inputs affected significance. Removing the outliers makes the relationship between conductivity and elevation significant (Table 3).

All six of the Colorado lakes that support *Acroloxus coloradensis* have glacial deposits along all, or a majority, of their shorelines (Table 2). Two of the capshell lakes are partially bordered by metamorphic or intrusive igneous

Table 2. Comparison of six Colorado lakes supporting *Acroloxus coloradensis* with 28 lakes in Rocky Mountain National Park (RMNP) where *A. coloradensis* was not found. (Calcium data are not available for five lakes sampled during 1997 and one lake sampled in 1993.)

Lake/coordinates	Elevation (m)	Surface area (ha)	Flushing rate index	Calcium (mg/L)	Conductivity (μmhos/cm)	Predominant surface geology unit
Finch Lake (105.5926°W, 40.1835°N)	3021	2.5	9.2	55	20	Till of Pinedale age
Lost Lake (105.6160°W, 39.9497°N)	2975	2.3	9.5	142	47	Glacial materials
Peterson Lake (105.5715°W, 39.9404°N)	2816	6.4	33.4	133	73	Glacial materials
Teal Lake (106.6075°W, 40.5836°N)	2686	5.3	5.7	91	38	Glacial deposits
Unnamed pond (105.5585°W, 40.1306°N)	2938	0.9	55.6	—	28	Till of Pinedale age
Upper Big Creek Lake (106.6167°W, 40.9132°N)	2746	44.3	50.3	101	28	Pleistocene till
Means	2864	10.3	27.3	104	39	
Means for 28 RMNP lakes lacking *A. coloradensis*	3074	2.8	116.7	49	24	
Significance (Kruskal-Wallis test)	H = 5.21 $p < 0.05$	H = 1.72 n.s.	H = 1.96 n.s.	H = 7.78 $p < 0.01$	H = 7.64 $p < 0.01$	

Table 3. Correlation coefficients between calcium concentrations, conductivity, and other physical attributes of Colorado lakes. Conductivity relationships include ten lakes that are not tabulated in Table 2. Analyses without roadside lakes omit Lily, Peterson, and Poudre Lakes, where traffic on adjacent highways may have affected calcium and conductivity values. Coefficients without asterisks are not statistically significant.

	Correlation coefficient	
Relationship	With roadside lakes	Without roadside lakes
Calcium concentration with		
Elevation	-0.57**	-0.53**
Flushing rate index	-0.09	-0.01
Surface area	0.32	0.36
Watershed area	0.03	0.14
Conductivity	0.87**	0.82**
Conductivity with		
Elevation	-0.35	-0.49**
Flushing rate index	-0.16	-0.17
Surface area	0.13	0.07
Watershed area	-0.11	-0.10

** $p< 0.01$

rock formations: Lost Lake has a small area identified as quartz monzonite group along its eastern shore (where *A. coloradensis* is present), and there is an area of hornblende gneiss along the north shore of Peterson Lake. Many lakes that do not support capshell populations also have glacial deposits along their shorelines, and there is no significant relationship between surface geology and the presence of *A. coloradensis* (Table 4). Lakes in the three surface geology categories do not differ significantly in terms of conductivity or elevation (Table 5).

The number of capshells on the Finch Lake artificial substrata has increased each year since the substrata were installed in 1994 (Table 6). There have been concurrent increases in the amount of visible algal growth on the substrata. On 26 Jul 1999, we counted 41 capshells on the substrata, which translates to a density of 27 capshells per m^2 of bottom surface area. This density is comparable to the estimate of 20 capshells/m^2 of lake bottom that Clarke

Table 4. Relationship between surface geology and the presence of *Acroloxus coloradensis*. Sample includes six Colorado lakes that support *A. coloradensis* and 28 lakes in Rocky Mountain National Park where *A. coloradensis* was not found. (Eight lakes are included in more than one surface geology category.) The relationship is not significant ($X^2 = 2.75$, $0.5 > p > 0.25$). Transported soils include map units designated as alluvium, alluvium/colluvium, till of Pinedale age (10,000-15,000 BP), till of Bull Lake age (130,000-150,000 BP), Pleistocene till, glacial deposits, and glacial materials. Metamorphic rock includes biotite schist, granitic gneiss, and hornblende gneiss. Intrusive igneous rock includes Silver Plume granite and quartz monzonite group.

	Surface geology category		
	Transported soils	Metamorphic rock	Intrusive igneous rock
Lakes with capshells	6	1	1
Lakes without capshells	15	14	5

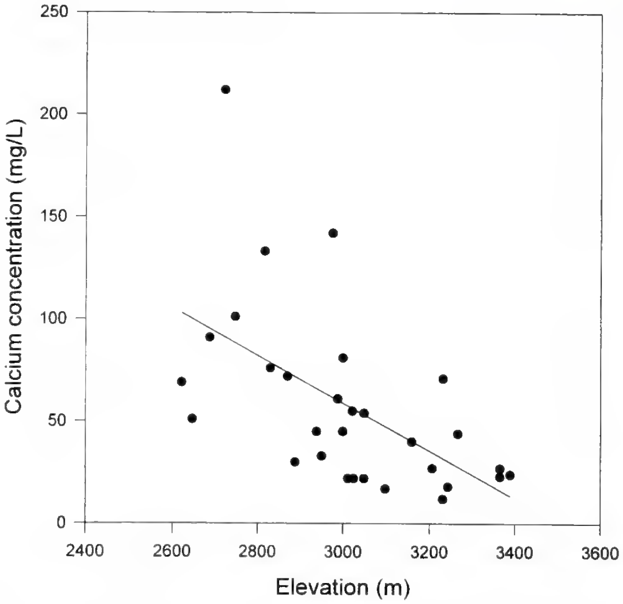

Fig. 1. Relationship between calcium concentrations and elevation in 30 Colorado lakes. The regression line explains 32.1 percent of the variance in calcium concentrations ($p < 0.01$). Analysis includes all lakes where calcium concentration was measured.

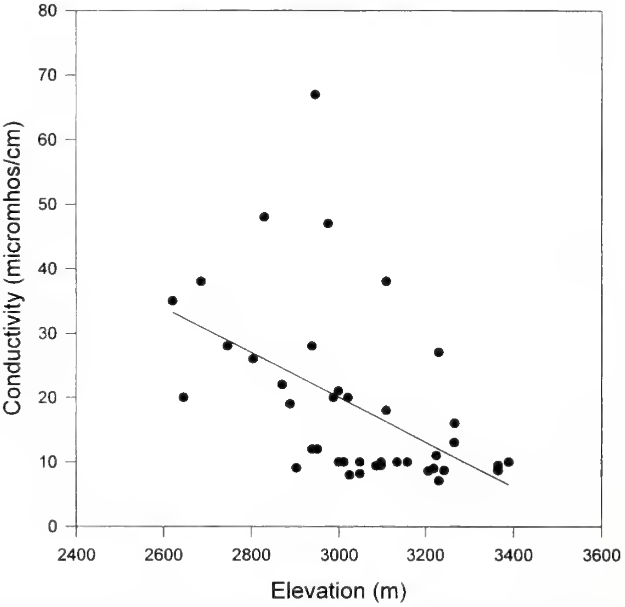

Fig. 2. Relationship between conductivity and elevation in 41 Colorado lakes. The regression line explains 24.4 percent of the variance in conductivity ($p < 0.01$). Analysis does not include three roadside lakes, where automobile traffic may have affected conductivity.

Table 5. Mean elevation and conductivity values (with standard deviations in parentheses) for lakes with different surface geology characteristics. Sample includes six Colorado lakes that support *Acroloxus coloradensis* and 28 lakes in Rocky Mountain National Park where *A. coloradensis* was not found. (Eight lakes are included in more than one surface geology category.) Conductivity data without roadside lakes omit Lily, Peterson, and Poudre Lakes, where traffic on adjacent highways may have affected values. The differences between the means are not significant ($p > 0.05$, Kruskal-Wallis test).

	Surface geology category						
	Transported soils		Metamorphic rock		Intrusive igneous rock		H
Elevation (m)	2978	(211)	3091	(162)	3099	(257)	3.20
Conductivity (µmhos/cm)							
All lakes	28	(25)	23	(29)	48	(71)	2.23
Without roadside lakes	21	(13)	16	(5)	19	(16)	4.06

(1993) reported for the Lost Lake, Montana, population. The average density on the ten substrata with the highest number of capshells (≥ 2 individuals/substratum) was 84 indiv/m^2. This latter value exceeds Bryce's (1970) estimate of 72 indiv/m^2 at favorable sites in Peterson Lake.

Table 7 summarizes the summer 1999 temperature records from Finch Lake and the unnamed pond. During the period we collected measurements (87 days in Finch Lake and 84 days in the unnamed pond), the average difference between daily high and low temperatures was 2.7°C in Finch Lake (logger depth = 72 cm) and 3.7°C in the unnamed pond (logger depth = 43 cm). There was also notable temperature variation associated with changing atmospheric conditions. When a winter storm moved into the area in late Sep, the Finch Lake temperature decreased 7.2°C over a 42-hour period, and the unnamed pond experienced a 7.6°C decrease.

DISCUSSION

The significantly higher calcium concentrations and conductivity values in capshell lakes (Table 2) suggest that dissolved ion concentrations may be an important variable affecting the distribution of *Acroloxus coloradensis.*

Table 6. Number and density of *Acroloxus coloradensis* on artificial substrata. Density measurements are per unit bottom surface area on the substrata. The substrata were placed in Finch Lake on 8 Jul 1994.

Sample date	Number of capshells	Density indiv/m^2
2 Aug 94	0	0.0
22 Aug 95	5	3.3
14 Aug 96	8	5.6
12 Aug 97	14	9.2
22 Aug 98	28	18.4
26 Jul 99	41	27.0

McKillop and Harrison (1972) found a similar relationship between calcium concentrations and the abundance of pulmonate gastropods at 31 sites in Ontario. They postulated three reasons that calcium concentrations might affect mollusc distributions: (1) gastropods need calcium for shell production, (2) physiologically harmful pH changes may occur at the organism-water interface in poorly buffered softwater, and (3) the abundance of food species may be limited by calcium. Because there were only minimal differences in water temperature and elevation among McKillop and Harrison's sample sites, the Ontario study separates the effect of calcium from the effects of tempera-

Table 7. Summer temperature conditions in two Colorado capshell lakes. Data collected by StowAway Tidbit temperature loggers mounted on the underside of artificial substrata.

Measurement	Finch Lake	Unnamed pond
Logger depth	72 cm	43 cm
Jul 1999		
Maximum temperature	18.2 C	19.4 C
Minimum temperature	12.9 C	10.9 C
Mean daily high temperature	16.4 C	17.0 C
Mean daily low temperature	14.3 C	13.5 C
Mean daily temperature range	2.1°C	3.5°C
Aug 1999		
Maximum temperature	17.0 C	19.1 C
Minimum temperature	11.4 C	10.6 C
Mean daily high temperature	15.8 C	16.7 C
Mean daily low temperature	13.2 C	13.0 C
Mean daily temperature range	2.6°C	3.7°C
Sep 1999		
Maximum temperature	16.4 C	16.7 C
Minimum temperature	3.1 C	1.6 C
Mean daily high temperature	12.2 C	12.3 C
Mean daily low temperature	9.0 C	8.5 C
Mean daily temperature range	3.2°C	3.8°C

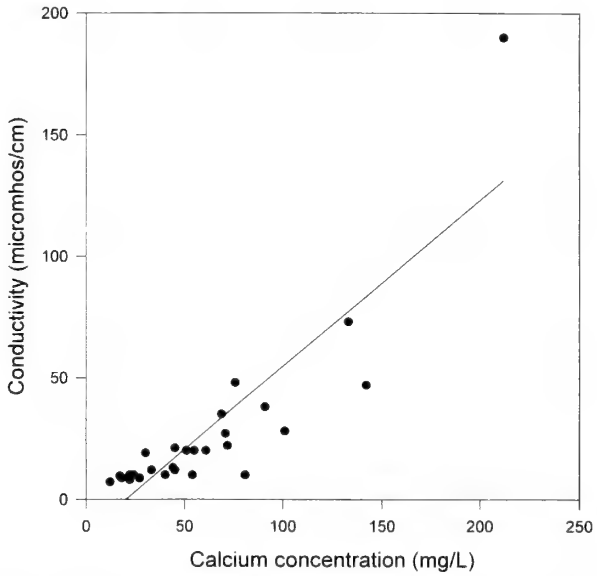

Fig. 3. Relationship between conductivity and calcium concentrations in 30 Colorado lakes. The regression line explains 76.3 percent of the variance in conductivity ($p < 0.01$). Analysis includes all lakes where calcium concentration was measured.

ture and elevation, which co-vary with calcium in our data.

Studies of the Loch Vale watershed in Rocky Mountain National Park suggest an explanation for the relationship between dissolved ion concentrations and elevation. Campbell *et al.* (1995) and Baron (1992) have found that dissolved ion concentrations in high-elevation streams drop steadily during late-spring and early-summer snowmelt and gradually recover after the winter snowpack has melted. A possible explanation is that snowmelt at higher elevations produces runoff that has little opportunity to pick up dissolved ions from thin and frozen (or non-existent) soil. Following snowmelt and thawing of the ground, subsurface runoff and groundwater seepage become the primary sources of water for the lakes. Movement of water through soil and bedrock substantially increases the concentration of dissolved ions. At lower elevations, gentler topography and thicker soils account for much greater quantities of dissolved ions. The reservoir of soil-derived ions presumably buffers low-elevation lakes from the seasonal variations observed at higher elevations (Fig 4).

Low concentrations of dissolved ions (some of which function as plant nutrients) may account for the clean, algae-free surfaces of rocks in high-elevation lakes.

As elevation decreases in the vicinity of Rocky Mountain National Park, lakes are increasingly likely to have mud or muck bottoms, rather than the rock (Clarke, 1981) or gravel (Paul and Clifford, 1991) substrata generally associated with capshells. The higher incidence of mud and muck bottoms is probably due to greater biological productivity and a larger input of small particles via runoff. The best habitat for *Acroloxus coloradensis* may be limited to a narrow elevational band between low-elevation lakes (which are unlikely to have rocky margins) and high-elevation lakes (which lack sufficient concentrations of dissolved ions).

During 1997 and 1998, Jacquie Lee (personal communication) found *Acroloxus coloradensis* in seven British Columbia lakes. Conductivity values in all seven lakes were ≥ 76.9 µmhos/cm (mean = 148 µmhos/cm), which is consistent with our observation that *A. coloradensis* is found in lakes with conductivity ≥ 20 µmhos/cm.

While it is tempting to relate capshell distributions to elevational variations in calcium concentrations, conductivity, and substratum composition, it is important to note that other elevation-related variables (e.g., temperature, season length) could also affect the distribution of *Acroloxus coloradensis.*

We were surprised by the magnitude of the daily temperature variations under the artificial substrata. The cyclic daily temperature changes suggest that solar radiation warms the upper surface of the substrata, and that heat is conducted to the lower surface (where *Acroloxus coloradensis* is most likely to be found). It appears that *A. coloradensis* is not restricted to subalpine lakes because it is a cold stenotherm.

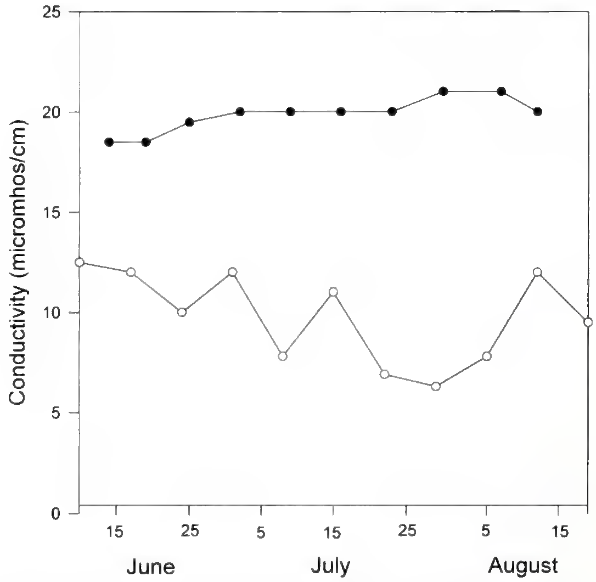

Fig. 4. Comparison of conductivity measurements in Finch Lake (3021 m, closed circles) and Loch Vale outlet (3097 m, open circles) during summer 1997. The Loch has a larger watershed area (663 ha vs. 23 ha), maximum watershed elevation (4009 m vs. 3158 m), and flushing rate index (123 vs. 9.2) than Finch Lake. Loch Vale data are from the Loch Vale Watershed Long-term Ecological Research and Monitoring Program, funded by the U. S. Geological Survey Biological Resources Division.

One of the reasons for installing the artificial substrata was to see if capshell densities are stable or if they undergo periodic oscillations. Variations in the difficulty of finding capshells in Peterson Lake suggest the latter possibility. Bryce (1970) noted that "many others" searched unsuccessfully for *Acroloxus coloradensis* in Peterson Lake after Henderson's initial collections (Walker, 1925). Capshells were relatively abundant during the 1960's when Bryce studied the population, but only three specimens were found during three days of searching in 1992 (Clarke, 1993). It is too early to tell whether capshell densities on the artificial substrata will eventually stabilize or if they will undergo periodic fluctuations.

The data in Table 2 suggest that the most-suitable habitat for Rocky Mountain (Colorado) populations of *Acroloxus coloradensis* appears to be in lakes at elevations between 2675 and 3025 m that have conductivity ≥ 20 μmhos/cm, calcium concentrations > 50 mg/L, and glacial deposits along at least part of their shorelines. Rocky substrata, small drainage basins, and macrophytic vegetation are often (but not always) associated with *A. coloradensis* habitat. Jacquie Lee (personal communication) has found *A. coloradensis* on submerged wood and leaves in four soft-bottomed British Columbia lakes. In two other lakes, she collected capshells from both rocks and submerged wood. Clarke (1993) has similarly found *A. coloradensis* in two mud-bottomed ponds in Ontario. Except for Upper Big Creek Lake, all of the Colorado capshell lakes - as well as Lost Lake, Montana, and the two lakes where Mozley (1930) found *A. coloradensis* in Jasper National Park, Alberta - have drainage basins smaller than 250 ha. The lack of macrophytic vegetation in the shallow margins of Upper Big Creek Lake and the sparse vegetation in Lost Lake, Montana (Russell and Brunson, 1967; personal observation), indicate that macrophytic vegetation is not an absolute requirement for *A. coloradensis*.

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A new hydrobiid snail from a saline spring in southern Alabama (Gastropoda, Prosobranchia, Rissooidea)

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Abstract: *Pseudotryonia grahamae* n. sp. is described from a saline spring in the Tombigbee River System in southern Alabama. It is most similar to *P. brevissima* (Pilsbry, 1890) from central Florida, but is distinguished by its larger shell with an indented parietal margin and its male reproductive system with two papillae along the inner curvature of the penis.

Key Words: Gastropoda, Hydrobiidae, *Pseudotryonia*, saline spring, Alabama

The North American freshwater snail fauna still remains largely unknown, with many species remaining to be described. Large geographic areas have not been surveyed adequately to document their faunas reliably, nor have unique habitats been examined sufficiently to reveal local endemics, such as the new species described below. Furthermore, a large diversity of species now buried as nomenclatorial synonyms remains to be recognized as valid (Thompson, 2000).

Alabama is one of the most extensively surveyed states in North America. It has long attracted the attention of naturalists because of the spectacular molluscan faunas of the Tennessee Alabama River basins. The diversity of unionid pelecypods and pleurocerid gastropods is unparalleled elsewhere. The major rivers then were exciting places for collecting mollusks. Virtually every shoal produced buckets of large and spectacularly ornate local endemics, all of which could be plucked from the substrate in large numbers and then graded for the choicest of specimens. Special techniques needed to collect smaller and more secretive species such as hydrobiids were seldom employed, because the diversity of the macro-fauna completely occupied the collector's time and attention. Smaller streams with their relatively depauperate faunas received little attention, and isolated springs were seldom visited. It is not surprising that novelties, such as the species described below, still remain to be discovered. The species described here is particularly interesting because of its habitat (Figs. 1-2) and its biogeographic affinities.

Pseudotryonia grahamae Thompson new species

Salt Spring Hydrobe

Diagnosis. A species of *Pseudotryonia* with three glandular penial lobes; one occurs near the middle of the outer curvature; two are juxtaposed on the inner curvature near the terminus. This snail differs from other known species by having two papillae along the inner curvature of the penis. The shell is distinct because of its convex spire, deeply impressed suture, adnate aperture, and rimate umbilicus. The shell is larger and has more whorls than similar species.

Shell. (Figs. 3-4, 6-17). Large, adult females up to 5.0 mm long with 5.5-6.4 whorls; males reach a length of 3.8 mm and have up to 5.3 whorls. Shell thin, hyaline, olivaceous gray. Shell elongate, about 0.46-0.56 times as wide as long. Spire convex in outline, particularly along the first four whorls; the last two whorls tend to become cylindrical. Suture deeply impressed. Initial protoconch whorl sharply protruding, 0.15 mm in diameter perpendicular to the initial suture. Subsequent whorls inflated; whorls of middle and lower spire shouldered and tending to be less convex below the periphery. Whorls nearly smooth, sculptured with fine, irregularly-spaced incremental striations, and much finer and more densely spaced segmented spiral striations. Umbilicus narrowly rimate; partially obstructed by the columellar margin of the peristome. Aperture subovate in shape; flattened along the parietal margin; height of aperture about 0.35-0.42 times the length of the shell. Axis of aperture inclined at about 11-18° to shell axis. Plane of

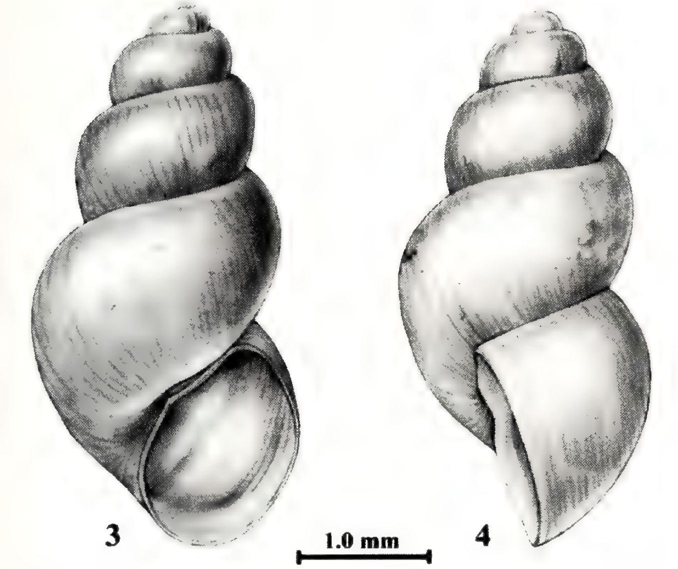
Figs. 1-2. Salt Springs, Clarke Co., Alabama. Scales are indicated by the 18 kg corgi dog in Figure 1 and the 3.8 liter plastic bucket in Figure 2.

aperture prosocline at about 16-23° to shell axis (Fig. 4). Peristome simple, thin and fragile, continuous across parietal margin, and tending to be solute from previous whorl in older specimens (Figs. 3, 11, 12); parietal margin arched forward near middle (Fig. 4).

Sexual Dimorphism. The shells are sexually dimorphic in shape and size. The sexes are readily distinguished even among juvenile shells. Females are more obese because of the slightly enlarged third whorl (Figs. 8-9). This is most apparent when the shell is viewed from the side posterior to the aperture. Males are more slender and tend to have a more noticeably impressed suture (Figs. 6-7). In order to verify gender the author selected 25 of the obese juvenile form and 25 of the slender juvenile form and denuded them of shells by placement in Bouin's Fixative. All had fewer than four whorls. The slender forms consisted of 24 males and one female. Among the obese forms 23 were females and two were males. The females larger than about 3.5 whorls in size and 1.5 mm long contain embryos in the uterus.

Adult females have a more robust apex than do males, but this is not as apparent in adults as it is among juveniles. Selected dried adult specimens were measured and the shells were dissolved in Bouin's Fixative in order to determine gender. Shells greater than 4.0 mm in length consistently were females. Adult male shells were difficult to recognize among shells less than 3.8 mm in length. Measurements for adult female and adult male shells are in Tables 1-3.

Anatomical Features. The head-foot of the animal is black with a light gray muzzle. The front and sides of the foot are also light gray. The tentacles are black with a



Figs. 3-4. *Pseudotryonia grahamae* new species. Holotype (UF 267620).

lighter basal zone, as well as a narrow gray band near the tip. The penis is light gray with darker pigmentation near its base. The mantle generally is light gray, as is the mantle collar. A transverse zone just posterior to the mantle collar, the area over the intestine, and the area over the digestive gland may be black, diffusely pigmented or light gray in color.

The penis (Fig. 5) is small and is located on the nape just to the right of the mid-dorsal line. It is strongly curved to the left when withdrawn beneath the mantle collar. The basal half is swollen and almost bulbous. The distal half is more slender and nearly uniform in width with a rounded apex that is nearly blunt. The penis bears three nearly equal-sized glandular lobes (gl), two along the inner curvature near the distal end, and another glandular lobe along the outer curvature just past the bulbous basal half. The glandular lobes are nearly equal-sized and are weakly constricted at their bases. The distal end of the penis bears a short acute terminal filament (tf). The vas deferens (vd) enters the base of the penis near the right margin. It is slightly convoluted, and it exits the penis through the terminal filament.

Type Locality. (Fig. 18). Alabama, Clarke Co., Salt Spring, Fred T. Simpson Wildlife Refuge, ca. 13.8 miles south-southeast of Jackson (31°22.7'N, 87°52.9'W) (FGT 5473).

Holotype. UF 267620; collected 31 August, 1994 by Fred G. Thompson, Richard Heard and Becky C. Graham.

Paratypes. UF 230742, USNM 860751 (ex UF 230742) (dry and wet), UF 230743, USNM 860752 (ex UF 230743) (dry and wet), UF 230744, USNM 860755 (ex UF 230744) (dry), USNM 860753 (dry), USNM 860754 (ex UF 230745) (dry), USNM 854832 (dry; DNA vouchers).

Table 1. *Pseudotryonia grahamae* n. sp. Shell measurements of holotype (UF 267620) and 10 adult female shells (UF 230744, Paratypes). L = standard length, W = standard width, AH = aperture height, AW = aperture width, Wh = whorls.

	L	W	AH	AW	Wh	W/L	AH/L	AW/AH	Wh/L
Holotype	4.29	2.11	1.58	1.28	5.40	0.49	0.37	0.79	1.26
min.	3.76	1.52	1.39	1.06	5.0	0.38	0.34	0.76	1.19
max.	4.36	2.11	1.58	1.25	5.5	0.53	0.39	0.86	1.41
mean	4.06	1.97	1.49	1.20	5.29	0.48	0.37	0.81	1.30
S.D.	0.19	0.16	0.06	0.06	0.14	0.04	0.01	0.03	0.06

Table 2. *Pseudotryonia grahamae* n. sp. Shell measurements of 20 adult female shells. (UF 258439, Paratypes). L = standard length, W = standard width, AH = aperture height, AW = aperture width, Wh = whorls.

	L	W	AH	AW	Wh	W/L	AH/L	AW/AH	Wh/L
min.	3.87	1.98	1.55	1.24	5.5	0.46	0.33	0.72	1.25
max.	4.96	2.36	1.74	1.36	6.3	0.56	0.44	0.83	1.43
mean	4.35	2.18	1.66	1.28	5.9	0.50	0.38	0.77	1.34
S.D.	0.33	0.10	0.08	0.04	0.3	0.03	0.03	0.03	0.08

Table 3. *Pseudotryonia grahamae* n. sp. Shell measurements of 10 adult male shells from Sta. 5627 (UF 258439, Paratypes). L = standard length, W = standard width, AH = aperture height, AW = aperture width, Wh = whorls.

	L	W	AH	AW	Wh	W/L	AH/L	AW/AH	Wh/L
min.	319	1.72	1.25	1.06	5.0	0.49	0.40	0.72	1.38
max.	3.76	1.98	1.55	1.22	5.3	0.56	0.44	0.85	1.60
mean	3.46	1.84	1.43	1.13	5.1	0.53	0.41	0.79	1.48
S.D.	0.21	0.08	0.11	0.05	0.09	0.02	0.02	0.05	0.08

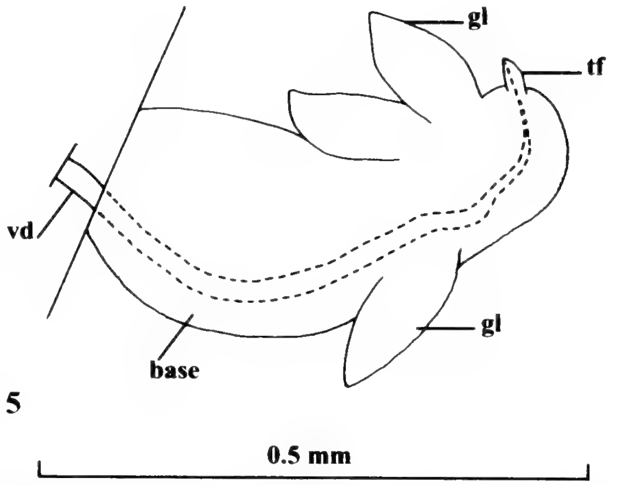
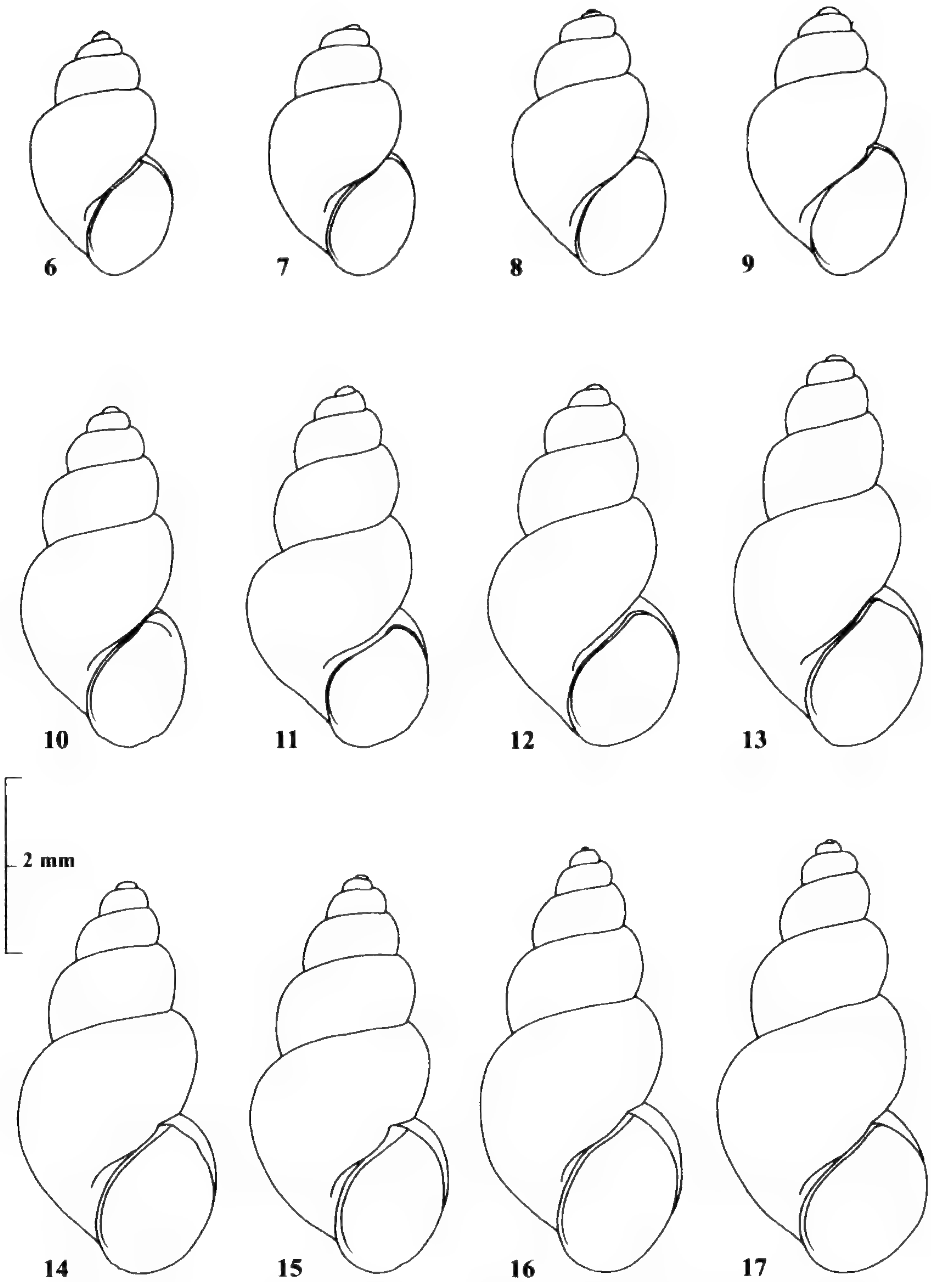


Fig. 5. *Pseudotryonia grahamae* new species. Penis: gl = glandular lobe; tf = terminal filament; vd = vas deferens.

Topotypic Paratypes collected 25 May, 1996: UF 258439.

Habitat and Distribution. (Figs. 1, 2, 18). Salt Spring originates from several seeps that flow into a circular mud flat that is ca. 100 m wide. Specimens comprising the paratype series UF 230743, UF 258439 were collected in the spring seeps. Specimens comprising the paratype series UF 230741 were collected from where the seeps converge to form a small shallow brook. The brook flows for ca. 300



Figs. 6-17. *Pseudotryonia grahamae* new species. Outline drawings of Paratypes collected from the spring seep shown in Fig. 2. Figs. 6-7: males (UF 230743). Figs. 8-13: females (UF 230743). Figs. 14-17: females (UF 258439).

m to a large, shallow pond, which in turn discharges into Salt Creek. The holotype and paratypes UF 230744 were collected from the shallow brook along a distance of approximately 100 m above the pond (Table 1). The creek in turn flows for ca. 3 miles west to its confluence with the Tombigbee River. *Pseudotryonia grahamae* is ubiquitous on the substrate from the seep area down to the pond. It was not found in the pond, but it was found in Salt Creek just above its confluence with the Tombigbee River (UF 230745). *P. grahamae* occurred in fine silt at all stations where it was encountered.

The geology of Salt Spring, the type locality, is discussed by Barksdale (1929). The spring issues from the Upper Eocene Hatchetigbee Formation. The Hatchigbee Formation forms the Hatchigbee Anticline that lies on a NW-SE axis, and extends over a distance of about 88

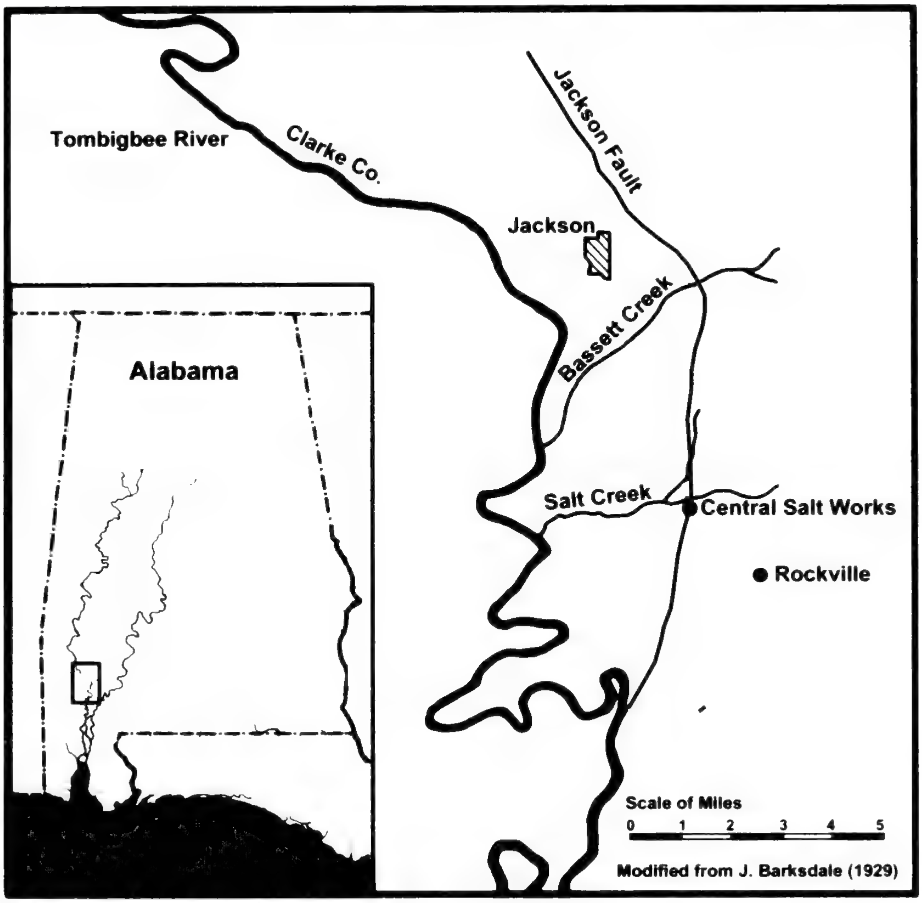


Fig. 18. Map showing the location of Salt Springs, the type locality of *Pseudotryonia grahamae* new species.

kilometers in the Jackson, Alabama area. The water from the spring has an alkalinity of up to 43 ppt. The spring is flooded periodically by the Tombigbee River during high water levels.

Relationships. Among known species *Pseudotryonia grahamae* is most similar to *P. brevissima* (Pilsbry, 1890) from central Florida (see Thompson, 1968:52-56; Hershler, 2001:15-19). Both species have a single glandular lobe along the middle of the outer curvature of the penis. *P. brevissima* has a single glandular lobe near the distal end of the inner curvature, whereas *P. grahamae* has two glandular lobes. The two species also share a deeply impressed suture separating the whorls of the shell. The shell of the new species is closely similar to that of *P. brevissima* because of its deeply impressed, channeled suture and by the convex outline of the spire. *P. grahamae* differs from *P. brevissima* by its larger, more attenuated shell, greater number of whorls, smaller aperture, and narrower umbilicus. The shell of large female *P. grahamae* is 4.0-5.0 mm long, with 5.4-6.3 whorls, and is about 0.46-0.56 times as wide as high, with the height of the aperture 0.33-0.44 times the length of the shell. In *P. grahamae* the umbilicus is reduced to a narrowly rimate perforation. By contrast the shell of large female *P. brevissima* is 3.5-4.4 mm long, with 4.5-5.1 whorls, and is 0.55-0.66 times as wide as long, with the height of the aperture 0.38-0.49 times the length of the shell. In *P. brevissima* the umbilicus is broadly perforate.

Etymology. This snail is named for Dr. Becky C. Graham, whose interest in the ecology of Salt Spring led to the discovery of this unusual snail.

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Distribution and Ecology of *Vertigo cristata* Sterki, 1919 in the Western Great Lakes Region

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Abstract: *Vertigo cristata*, previously unreported from the U. S. A., was located at 84 sites in northern Minnesota, northern and southwestern Wisconsin, the Upper Peninsula of Michigan, and also in Ontario on Manitoulin Island and the northern tip of the Bruce Peninsula. It was found in nine habitats (carbonate cliffs, lakeshore carbonate ledges, igneous cliffs, sandstone cliffs, rocky woodlands, igneous lakeshore outcrops, swamp forests, tamarack wetlands, and white cedar wetlands) and was essentially confined to areas north of 45°N. It was most frequently encountered on igneous rock outcrops, where it was observed in over 67% of surveyed sites. *V. cristata* individuals were easily separated from *V. gouldi* (A. Binney, 1843), with which it has often been lumped as a subspecies, as well as from other central U. S. *Vertigo* taxa, including *V. modesta modesta, V. paradoxa*, and *V. meramecensis*.

Key Words: *Vertigo cristata*, Great Lakes, biogeography, ecology

Vertigo cristata was first described (as *V. gouldi cristata*) by Sterki in 1919 from Quebec. Pilsbry (1948) considered it a 'strongly marked' race, and listed an additional site along the north shore of Lake Superior. Oughton (1948) reported it from 'probably the entire province' of Ontario, but expressed difficulty separating it from *V. gouldi* and *V. paradoxa*. Frest and Johannes (1991) treated *V. cristata* as a full species when comparing it to Black Hills *V. paradoxa. V. cristata* has not been reported from regions to the south (eastern U.S.: Hubricht, 1985), east (New Brunswick: Clarke *et al.* 1968), or west (Alberta: Platt, 1980; Van Es and Boag, 1981) of the Great Lakes.

In the course of analyzing land snail faunas in the western Great Lakes region, we encountered individuals referable to *Vertigo cristata* at 84 stations. Using these observations, a more thorough consideration can be made of its: (1) distribution; (2) shell morphology; (3) preferred habitats; and (4) molluscan associates.

METHODS AND MATERIALS

A total of 324 sites were surveyed for their terrestrial gastropod faunas within the states and provinces of Illinois, Iowa, Michigan, Minnesota, Ontario, New York, and Wisconsin. Sites were chosen for survey if they represented typical examples of their respective habitat, and (except for anthropogenic sites) were undisturbed. Collections were made from 22 discrete habitat types, including carbonate cliffs, lakeshore carbonate ledges, igneous cliffs, algific talus slopes, fens, lakeshore alluvial banks, rocky woodlands, calcareous open meadows, lowland woods, alvars, cobble beaches, shale cliffs, carbonate glades, old fields, tallgrass prairie, aspen parklands, sandstone cliffs, and open dunes. Descriptions of these habitat types are found in Nekola (1999). The location of each sample was marked on USGS (or equivalent) 7.5 minute topographic maps and digitized.

Documentation of terrestrial gastropods from each site was accomplished through standard soil litter sampling procedures, as outlined in Nekola (1999). All recovered, identifiable shells from each site were assigned to species (or subspecies) using the author's reference collection and the Hubricht collection at the Field Museum of Natural History. All specimens have been catalogued and are housed in collections maintained at the University of Wisconsin - Green Bay.

RESULTS AND DISCUSSION

Distribution

The 84 encountered *Vertigo cristata* populations were found in all four major political divisions of the western Great Lakes: 37 from northern Minnesota, 22 from the

Table 1. *Vertigo cristata* occurrences in the western Great Lakes region.

State / Province	# occurrences	# sampled	% occurrence
Minnesota	37	52	71.2
Michigan	22	82	25.9
Wisconsin	20	204	9.8
Ontario	5	22	22.3

Upper Peninsula of Michigan, 20 from northern and southwestern Wisconsin, and five from southern Ontario on Manitoulin Island and the Bruce Peninsula (Table 1; Fig. 1). The southernmost population occurs on a north-facing sandstone cliff at Camp Douglas in southwestern Wisconsin (43°55'N). The next most southern populations occur on wooded lakeshore carbonate outcrops at Toft Point (45°4'N), Marshall's Point (45°8'N) and Peninsula State Park on the Door Peninsula in northeastern Wisconsin (45°9'N) and on the northern tip of the Bruce Peninsula in Ontario (45°14'N). The Michigan, Minnesota, and Wisconsin populations represent the first reported modern occurrences of this taxon from the U. S. A.

The occurrence frequency of *Vertigo cristata* among all sampled sites in these states and provinces ranged from almost 10% in Wisconsin to 71% in Minnesota. The high frequency of this taxon within Minnesota is likely due to the facts that: (1) all sites inventoried were north of 45°N; and (2) the great majority of sampled habitats represented bedrock outcrops. The apparent limitation of *V. cristata* in this survey to areas near the Great Lakes is almost certainly an artifact of the sampling regime, which principally targeted sites with high-Ca bedrock exposures (carbonate or mafic/ultramafic igneous rock). In this region, such habitats are most commonly encountered within 40 km of the lakeshore.

The presence of *Vertigo cristata* at lower frequencies in other forested habitats (see below) suggests that it will eventually be found throughout a region bordered to the south by 45°N, to the east by the eastern border of the Province of Quebec, and to the west by the aspen parklands and tallgrass prairie of Manitoba and northwestern Minnesota. Current and historical data do not clearly indicate how far north and northwest this taxon will be found in Quebec, Ontario, and Manitoba, although it seems probable that it will occur north to forest-tundra border along the southern shore of Hudson Bay. Outlying populations at or south of 45°N are likely limited to areas that are microclimatically protected from warm summer temperatures. The southernmost Wisconsin and Ontario sites are limited to areas adjacent to the Great Lakes shore and/or north-facing cliffs. Maximum summer temperatures of lakeshore habitats are known to be depressed over areas farther inland due to their proximity to cold lake waters (Curtis, 1959).

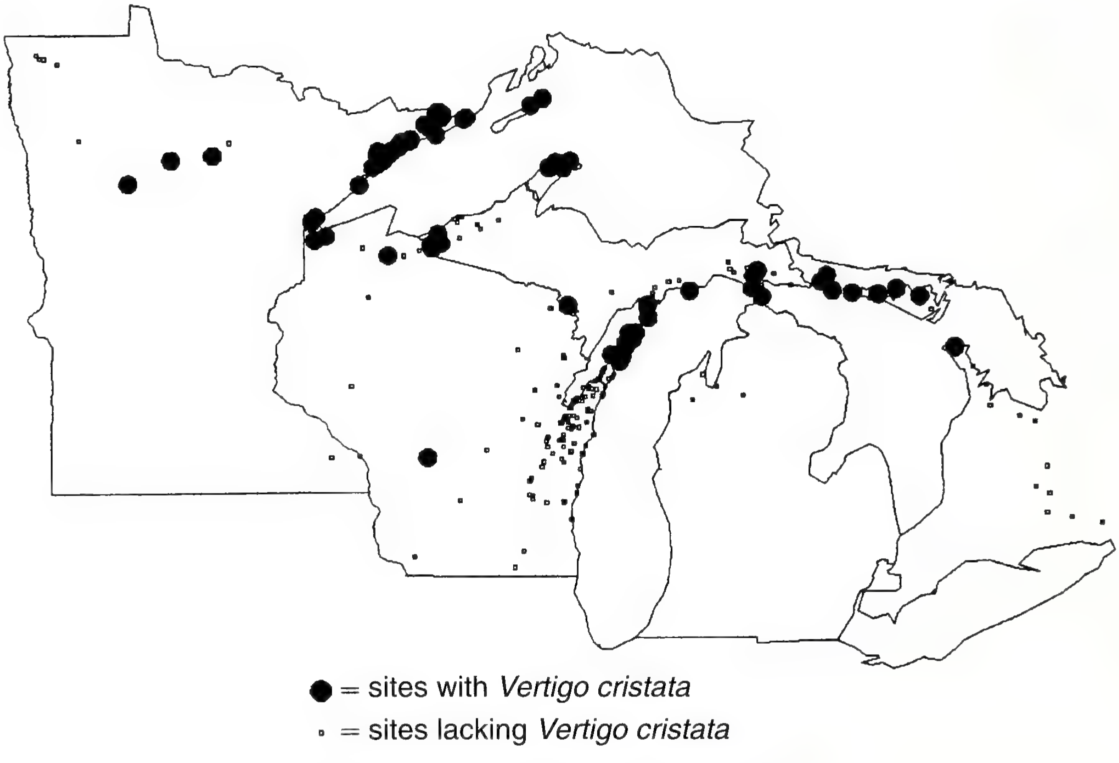
● = sites with *Vertigo cristata*
▫ = sites lacking *Vertigo cristata*

Fig. 1. *Vertigo cristata* distribution in the western Great Lakes.

Shell Morphology

Vertigo cristata was clearly marked and distinct. As such, I follow Frest and Johannes (1991) in considering it a full species. *V. cristata* is easily distinguished from *V. gouldi* (Fig. 2) by: (1) never possessing a basal lamella; (2) possessing a strong crest; (3) having the parietal lamella pointed towards the lower palatal, rather than the upper palatal (as in *V. gouldi*); and (4) having more closely spaced, regular, and sharp shell striations. Unlike Oughton (1948), I did not observe any individuals intermediate between *V. cristata* and *V. gouldi*, even at the 23 sites of co-occurrence. As I have not yet analyzed Oughton's material, the disposition of his intermediate individuals remains unclear. While Oughton reported *V. cristata* from 'probably the entire province,' I have been unable to locate it in Ontario south of the northernmost tip of the Bruce Peninsula. As such, his intermediate individuals may likely represent misidentified *V. bollesiana, V. gouldi,* or *V. paradoxa*, taxa that are more broadly distributed in southern Ontario.

Considerably more trouble was encountered in separating some of the largest *Vertigo cristata* individuals from the smallest *V. modesta modesta*. These two taxa were distinguished by the weaker crest (when present), more irregular shell striations, and more massive apertural lamellae of *V. m. modesta* as compared to *V. cristata* (Fig. 2). Additionally, a few individuals were found to approach *V. paradoxa* somewhat in appearance. These two taxa were distinguished using the more deeply set lower palatal lamella as compared to the upper, and lack of a crest in *V. paradoxa. V. cristata*, however, has a strong crest and lower and upper palatal lamellae set at equal depths into the aperture.

In eastern North America, *Vertigo cristata* appears

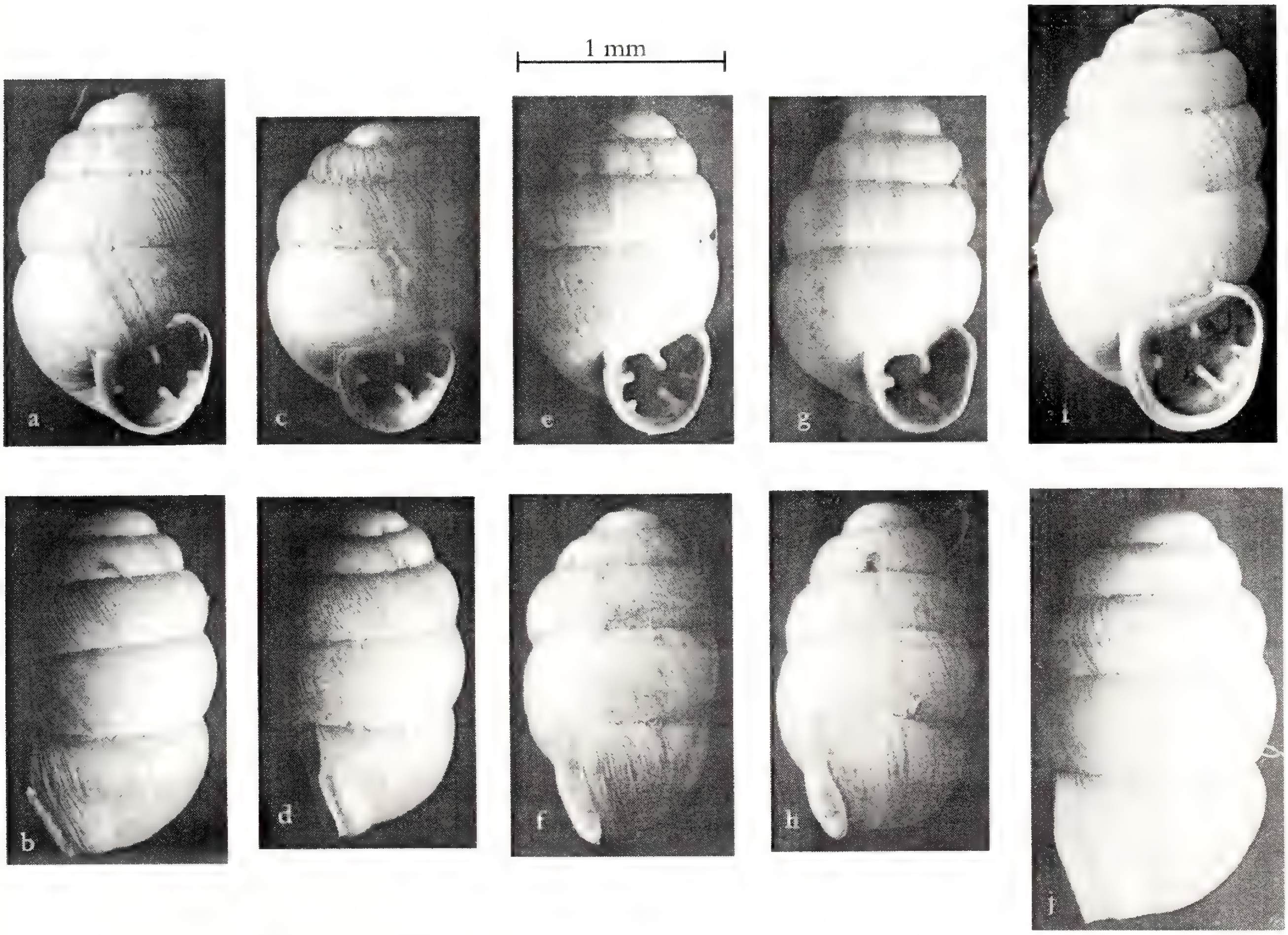

Fig. 2. Scanning electron micrographs of *Vertigo cristata* and related taxa. **a, b:** *V. cristata*, Mt. Josephine, Cook County, Minnesota, U. S. A. (89°39'14" W, 47°58'50" N), JCN #4559. **c, d:** *V. cristata*, Toft Point, Door County, Wisconsin, U. S. A. (87°5'5" W, 45°4'40" N), JCN #1061. **e, f:** *V. gouldi*, Toft Point, Door County, Wisconsin, U. S. A. (87°5'5" W, 45°4'40" N), JCN #1062. **g, h:** *V. meramecensis*, Dark Hollow, Linn County, Iowa, U. S. A. (91°30' W, 41°53'54" N), JCN #376. **i, j:** *V. modesta modesta*, Metcalf Rock, Grey County, Ontario, Canada (80°26'31" W, 44°25'3" N), JCN #2543. Micrographs were taken with a Hitachi S-2460N Scanning Electron Microscope in N-SEM Mode (10 Pa; 22 kV) with a backscatter detector and #2 Gamma Correction. JCN = author's collection accession number.

most similar to *V. meramecensis* VanDevender, 1979, which occurs in the Ozark Plateau of Missouri and Arkansas (Hubricht, 1985; Brian Coles, pers. comm.) and the Paleozoic Plateau of northeastern Iowa, southeastern Minnesota, and northwestern Illinois (Frest, 1986, 1991). Both of these taxa range from 1.7-2.2 mm in size, have strong shell striations, and possess four principle apertural lamellae, with the parietal being pointed at the lower palatal (Fig. 2). However, *V. meramecensis* differs from *V. cristata* in: (1) lacking a crest; (2) having a dark cinnamon-red shell color (rather than yellowish); (3) occasionally possessing a weak basal lamella; and (4) having the body whorl being wider than the penultimate (Frest and Fay, 1981). While no co-occurring populations of *V. cristata* and *V. meramecensis* were found, both taxa occur on cool cliffs in the Paleozoic Plateau, and such sites may eventually be located in southeastern Minnesota or southwestern Wisconsin.

Shells of *Vertigo cristata* fell into two size classes, with one ranging from 1.7-1.9 mm, and another from 2.1-2.2 mm (Fig. 2). The larger form appeared limited to northeastern Minnesota and the Keweenaw Peninsula of Michigan. As shells in these two groups appeared to be otherwise identical, these races were not considered separate taxonomic entities. However, further morphometric and genetic analyses may be warranted to help elucidate their true status.

Habitat Preferences

Vertigo cristata populations were located from 9 different habitats (Table 2), with a preference being shown for wooded outcrops of igneous rock: 67% of surveyed igneous bedrock outcrop sites supported populations, followed by igneous lakeshore outcrops (50%), sandstone cliffs (50%), carbonate lakeshore ledges (43.5%), white cedar wetlands (13.3%), carbonate cliffs (12.6%), tamarack wetlands (10.3%), rocky woodlands (8%), and swamp forest (6.3%). Most sites were wooded, with eastern white cedar (*Thuja occidentalis* L.) being commonly present. On bedrock outcrops, *V. cristata* was most often found on soil-covered ledges, while in wetland sites it was most frequently encountered in deciduous leaf accumulations above the high-water line.

Table 2. Habitats of *Vertigo cristata* in the western Great Lakes region.

Habitat type	# occurrences	# sampled	% occurrence
Igneous Cliff	50	74	67.6
Carbonate Cliff	13	103	13.7
Carbonate Lakeshore Ledge	10	23	31.6
Tamarack Wetland	3	29	5.0
Rocky Woodland	2	26	9.1
White Cedar Wetland	2	15	20.0
Igneous Shoreline	2	4	50.0
Sandstone Cliff	1	2	50.0
Swamp Forest	1	16	6.3

Associated Species

Across all habitats, 54 land snail species were found to co-occur with *Vertigo cristata* (Table 3). Eight of these (*Discus catskillensis, Zonitoides arboreus, Striatura milium, Nesovitrea binneyana, Punctum minutissimum, Euconulus fulvus, V. paradoxa*, and *Strobilops labyrinthica*) were found in 50% or more of the *V. cristata* sites. Of the remaining, 39 (over 70% of the total) were found in fewer than 25% of *V. cristata* sites. None of these associated taxa was found only with *V. cristata*.

The number of co-occurring taxa ranged from 41 in carbonate cliffs to 12 in igneous lakeshore outcrops (Table 3). Mean richness for sites supporting *Vertigo cristata* varied from 25 in swamp forest and 18.5 on carbonate cliffs to 9.5 and 9.4 on igneous lakeshore outcrops and cliffs. A significant reduction in species richness with increasing latitude has been previously shown for land snail communities within the Western Great Lakes region (Nekola, 1999). In addition, the sites where *V. cristata* is most frequently encountered are also, on average, the most species-poor.

The habitats supporting *Vertigo cristata* have two general assemblages (Table 3). Wooded rock outcrop sites (carbonate cliffs, carbonate lakeshore ledges, igneous cliffs, sandstone cliffs, rocky woodlands, and igneous lakeshore outcrops) support not only the most common associates, but also typical western Great Lakes region wooded bedrock outcrop taxa such as *Anguispira alternata, Carychium exile, Helicodiscus shimeki, Paravitrea multidentata, Stenotrema fraternum, V. bollesiana, V. gouldi, V. hubrichti*, and *Zoogenetes harpa*. Wooded wetland habitats for *V. cristata* (swamp forest, tamarack wetland, and white cedar wetland), harbored the most common associates as well as typical western Great Lakes region wooded wetland taxa such as *C. exiguum, Euconulus alderi, Gastrocopta tappaniana, V. elatior*, and *V. nylanderi*.

Most of the associated species have northeastern or cosmopolitan modern ranges (Hubricht, 1985). However, seven (*Hendersonia occulta, Vallonia gracilicosta, Vertigo hubrichti, V. modesta modesta, V. modesta parietalis, Vertigo* n.sp. *sensu* Frest, 1991, and *V. paradoxa*) had extensive eastern U.S. ranges during the late Pleistocene, even though they are largely limited in modern times to the Great Lakes region (Frest, 1991; Frest and Johannes, 1991). Given that almost 15% of *V. cristata*'s associates represent such potential glacial relicts, it is surprising that it is not more strongly represented in the Pleistocene record. Neither Hubricht (1985) nor Frest and Dickson (1986) report Pleistocene fossil sites. The only published fossil

Table 3. Species associated with *Vertigo cristata* in the western Great Lakes region. Nomenclature follows Hubricht (1985). Habitats are: 1 = Carbonate Cliff, 2 = Carbonate Lakeshore Ledge,3 = Igneous Cliff, 4 = Sandstone Cliff, 5 = Rocky Woods, 6 = Igneous Lakeshore Outcrop, 7 = Swamp Forest, 8 = Tamarack Wetland, 9 = White Cedar Wetland.

Species	Number of Occurrences in Habitat:									
	1	2	3	4	5	6	7	8	9	Total
Discus catskillensis (Pilsbry, 1898)	13	9	43	1	2	2	1	3	2	76
Zonitoides arboreus (Say, 1816)	12	9	44	1	2		1	2	2	73
Striatura milium (Morse, 1859)	10	10	31	1	2	2	1	3	1	61
Nesovitrea binneyana (Morse, 1864)	8	6	40	1		1	1	2	1	60
Punctum minutissimum (I.Lea, 1841)	13	10	24	1	2	2	1	3	2	58
Euconulus fulvus (Müller, 1774)	11	9	25	1	1	1		1		49
Vertigo paradoxa Sterki, 1900	9	2	29		1	1		1		43
Strobilops labyrinthica (Say, 1817)	12	8	13	1	2	1	1	2	2	42
Anguispira alternata (Say, 1817)	13	9	18		1					41
Columella simplex (Gould, 1841)	10	9	12	1	2	1	1	2	1	39
Zoogenetes harpa (Say, 1824)	1	1	29		2	2				35
Striatura exigua (Stimpson, 1847)	3	4	20		1	1	1	3	1	34
Vertigo gouldi (A. Binney, 1843)	13	8	5		1					27
Helicodiscus shimeki Hubricht, 1962	7	8	8					1	1	25
Carychium exile H.C.Lea, 1842	5	5	9				1	2	1	23
Discus whitneyi (Newcomb, 1864) [= *Discus cronkhitei* (Newcomb, 1865)]	5	2	10					2		19
Vertigo bollesiana (Morse, 1865)	6	6	5							17
Helicodiscus parallelus (Say, 1817)	3	2	4	1	2	2	1			15
Vertigo hubrichti (Pilsbry, 1934)	8	7								15
Nesovitrea electrina (Gould, 1841)	1	1	6				1	3	1	13
Paravitrea multidentata (A. Binney, 1840)	6	2	3		1					12
Succinea ovalis Say, 1817	2	1	9							12
Vallonia gracilicosta Reinhardt, 1883	9	1					1	1		12
Vertigo n.sp. *sensu* Frest, 1991	7	5								12
Cochlicopa lubrica (Müller, 1774)	1	1	5	1	1			1	1	11
Gastrocopta pentodon (Say, 1821)	5	1	3	1			1			11
Glyphyalinia indentata (Say, 1823)	5	1	1	1	1					9
Planogyra asteriscus (Morse, 1857)		3	3					1	2	9
Striatura ferrea Morse, 1864		3	3	2					1	9
Stenotrema fraternum fraternum (Say, 1824)	5	2	1							8
Carychium exiguum (Say, 1822)							1	3	2	6
Cochlicopa lubricella (Porro, 1838)			2	1	1		1			6
Gastrocopta contracta (Say, 1822)	4			1			1			6
Vitrina limpida Gould, 1850	3		1		1	1				6
Euconulus polygyratus (Pilsbry, 1899)	2	2			1					5
Vertigo modesta modesta (Say, 1824)	1		4							5
Deroceras laeve (Müler, 1774)	2		1				1			4
Euconulus alderi (Gray, 1840)							1	2	1	4
Gastrocopta tappaniana (C.B. Adams, 1842)							1	3		4
Neohelix albolabris (Say, 1816) [= *Triodopsis albolabris*]	2	2								4
Vallonia costata (Müller, 1774)	1	2								3
Vertigo elatior Sterki, 1894							1	2		3
V. modesta parietalis (Ancey, 1887)			3							3
V. nylanderi Sterki, 1909							1	2		3
Cochlicopa morseana (Doherty, 1878)	1		1							2
Glyphyalinia rhoadsi (Pilsbry, 1899)	1	1								2
Hawaiia minuscula (A. Binney, 1840)				1			1			2
Catinella avara (Say, 1824)							1			1
Gastrocopta holzingeri (Sterki, 1889)	1									1
Guppya sterkii (Dall, 1888)	1									1
Hendersonia occulta (Say, 1831)	1									1
Punctum n.sp. *sensu* Frest, 1990							1			1
Vallonia pulchella (Müller, 1774)								1		1
Vertigo arthuri (von Martens, 1884)								1		1
Total Number of Associates	41	34	32	15	19	12	24	24	16	
Average Species Richness per Site	18.5	16.9	9.4	16	14.5	9.5	25	16.7	12	

occurrence is from Illinoian-age sediments in southern Illinois (Miller *et al.*, 1994). This situation is reminiscent of *V. meramecensis*, which also regularly occurs with glacial relict taxa, but is unknown from Pleistocene sediments (Frest and Fay, 1981).

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Distribution and ecology of *Vertigo nylanderi* Sterki, 1909 in the Western Great Lakes region

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Abstract: The land snail *Vertigo nylanderi,* previously reported from only six modern global sites, was located at 22 stations in north-central Minnesota, northern Michigan, and eastern Wisconsin. Its populations are limited to nutrient-rich, forested wetlands (typically dominated by Tamarack or Black Ash) that are underlain by calcareous substrates. Most sites are within 40 km of the Lake Michigan and Lake Huron shorelines. This species was found to be morphologically distinct from other conchologically similar taxa such as *V. arthuri* (von Martens, 1884), *V. hubrichti* (Pilsbry, 1934), and *V. paradoxa* Sterki, 1900. Although 54 other terrestrial gastropod taxa have been observed to coexist with *V. nylanderi*, only 12 of these occur in at least 50% of sites. The cool, wet, calcareous habitats that support *V. nylanderi* appear to be similar to late Pleistocene environments, and it is possible that this species represents a relict from that period.

Key Words: *Vertigo nylanderi*, Great Lakes, biogeography, ecology, glacial relict

Vertigo nylanderi is a minute and poorly known land snail of eastern North America. Until recently only six modern stations were known: the type location at Woodland in Aroostook County, Maine (Pilsbry, 1948), three sites in eastern Ontario (Onakawana, Cochrane District; Ottawa, Carleton County; Temagami Provincial Forest, Nipissing District; Oughton, 1948), Wilderness State Park in the northern Lower Peninsula of Michigan (Burch and Jung, 1988), and Lake Itasca State Park in Clearwater County, Minnesota (Dawley, 1955). Only one of these collections (Wilderness State Park) was made since 1949. Hubricht (1985) reported having never observed it in over 40 years of collecting within the eastern United States.

Little also has been reported of the preferred habitats for *Vertigo nylanderi*. No habitat information was provided for the Wilderness State Park, Lake Itasca or type stations. Oughton (1948) describes the region in the Temagami Provincial forest where *V. nylanderi* occurs (Olive Township) as having alkaline soils with pH values ranging from $6^1/_2$-7, but provided no other information regarding this, or any other, of the Ontario sites.

During a study of land snail communities within the Great Lakes region, 22 extant stations for *Vertigo nylanderi* were located. These allow for the first time a more thorough consideration of this species: (1) distribution in the Great Lakes region; (2) shell morphology; (3) habitats; (4) molluscan associates; and (5) Pleistocene history.

METHODS AND MATERIALS

A total of 424 sites were surveyed for their terrestrial gastropods across a 1300x1000 km region, including portions of Illinois, Michigan, Minnesota, New York, southern Ontario, and Wisconsin. Sites were chosen for survey if they represented typical examples of their respective habitat type, and (except for anthropogenic habitats) were undisturbed. Collections were made from 21 discrete habitat types including carbonate cliffs, lakeshore carbonate ledges, igneous cliffs, algific talus slopes, fens, lakeshore alluvial banks, rocky woodlands, calcareous open meadows, lowland woods, alvars, cobble beaches, shale cliffs, carbonate glades, aspen parkland, old fields, tallgrass prairie, and open dunes. Descriptions these habitat types are found in Nekola (1999). The location of each sample was marked on USGS 7.5 minute (or equivalent) topographic maps, and latitude-longitude coordinates determined through digitization of these maps using the ATLAS DRAW software package.

Documentation of terrestrial gastropods from each site was accomplished through standard soil litter sampling procedures, as outlined in Nekola (1999). All recovered, identifiable shells from each site were assigned to species (or subspecies) using the author's reference collection and the Hubricht collection at the Field Museum of Natural History. All specimens have been catalogued and are housed in collections maintained at the University of Wisconsin - Green Bay.

RESULTS AND DISCUSSION

Distribution

Although the 22 identified populations (Table 1) generally fall within the previously known range of *Vertigo nylanderi* (northern Maine to James Bay to northwestern Minnesota), they verify for the first time its presence within Wisconsin and the Upper Peninsula of Michigan. All of these populations are confined to sites underlain by calcareous substrates (bedrock, glacial till, or lacustrine sediments). In Michigan and Wisconsin, most sites are within 40 km of the Lake Michigan or Lake Huron shoreline

Table 1. Extant stations for *Vertigo nylanderi* in the western Great Lakes region.

Site	Location	Wetland Habitat Type	Collection Date	# Adults
MICHIGAN				
Chippewa County				
Maxton Plains Center 2	84° 39' 24" W, 46° 4' 44" N	Tamarack - Sedge	June 17, 1998	4
Prentiss Bay	84° 13' 49" W, 46° 59' 25" N	Tamarack - Sedge	June 19, 1998	4
Delta County				
Garden Corners	87° 32' 4" W, 46° 53' 23" N	Tamarack - Sedge	June 27, 1998	1
Kalkaska County				
Angling Swamp	85° 1' 14" W, 45° 40' 14" N	Tamarack - Sedge	July 24, 1999	13
Mackinac County				
Townhall Road	85° 10' 28" W, 46° 8' 19" N	White Cedar - Tamarack	June 20, 1998	1
Schoolcraft County				
Birch Creek	86° 26' 35" W, 46° 47' 16" N	Tamarack - Sedge	July 14, 1999	4
MINNESOTA				
Beltrami County				
Pennington Bog	94° 28' 44" W, 47° 29' 59" N	White Cedar - Tamarack	July 29, 1999	4
Clearwater County				
Iron Springs	95° 15' 5" W, 47° 15' 11" N	Tamarack - Sedge	July 27, 1999	6
Bear Paw Point W	95° 11' 51" W, 47° 13' 23" N	Black Ash	July 27, 1999	1
Bear Paw Point E	95° 11' 41" W, 47° 13' 11" N	Black Ash - Tamarack	July 29, 1999	20
Itasca County				
Bowstring	94° 47' 43" W, 48° 33' 11" N	Tamarack - Sedge	July 29, 1999	3
WISCONSIN				
Brown County				
Lily Lake County Park	88° 51' 3" W, 44° 25' 19" N	Tamarack - Sedge	June 13, 1998	1
Lily Lake County Park	88° 51' 3" W, 44° 25' 22" N	White Cedar - Yellow Birch	June 13, 1998	1
Reforestation Camp	88° 5' 37" W, 45° 39' 36" N	White Cedar - Black Ash	December 11, 1999	2
Calumet County				
East River Road	88° 3' 42" W, 44° 8' 21" N	Tamarack - Sedge	November 15, 1998	1
Kiel Marsh	88° 3' 34" W, 44° 53' 52" N	Tamarack - Black Ash	October 29, 1998	12
Door County				
Corbisier Farm	88° 32' 57" W, 45° 45' 17" N	White Cedar Stonepile	October 25, 1998	26
Toft Point	87° 5' 52" W, 45° 4' 43" N	Tamarack - Sedge	October 11, 1997	2
Kewaunee County				
Tisch Mills 1	88° 38' 21" W, 44° 20' 46" N	Tamarack - Sedge	November 7, 1998	3
Tisch Mills 2	88° 38' 21" W, 44° 20' 50" N	White Cedar - Tamarack	November 7, 1998	1
Manitowoc County				
Zander Road	88° 52' 44" W, 44° 18' 32" N	Black Ash	October 4, 1998	1
Oconto County				
Morgan Marsh	88° 8' 10" W, 45° 47' 32" N	Alder - Tamarack	October 31, 1998	1

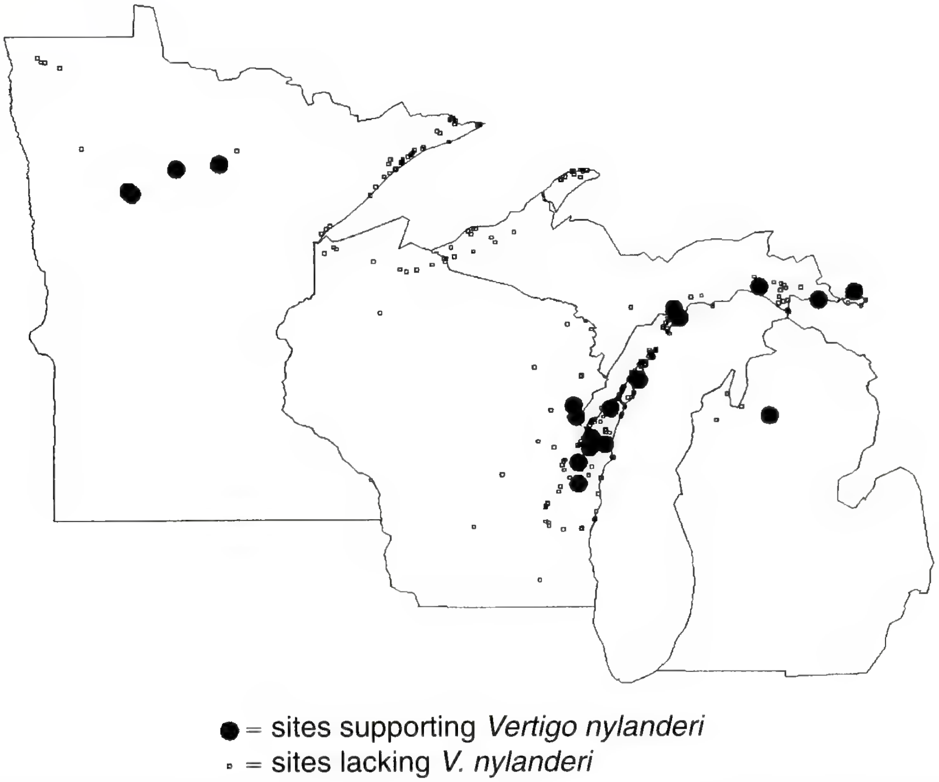
● = sites supporting *Vertigo nylanderi*
▫ = sites lacking *V. nylanderi*

Fig. 1. *Vertigo nylanderi* distribution in the western Great Lakes. As some stations are close together (Lily Lake 1 and 2, Tisch Mills 1 and 2, and Bear Paw Point E, Bear Paw Pt W, and Iron Springs), their occurrence dots overlap. As such, only 18 separate occurrences are apparent at this map scale.

(Fig. 1).

The previously documented populations are also apparently confined to areas underlain by calcareous bedrock or till. The type location in Aroostook County, Maine rests atop Silurian and Ordovician limestones (Osberg *et al.*, 1985). The Ottawa and Onakawana sites in Ontario rest above limestone, while the Temagami Provincial Forest site has calcareous soils (Oughton, 1948). The Lake Itasca area is covered by tills from the Des Moines lobe, which is largely composed of limestone and shale (Ojakangas and Matsch, 1982).

While Levi & Levi (1950) listed *Vertigo nylanderi* from Peninsula State Park in Door County, Wisconsin, these data suggest that this report is almost certainly in error. No appropriate habitats for *V. nylanderi* are known from the park, and we have not been able to locate it there. It seems likely that their report was based on the closely related *V. hubrichti*, which is frequent on limestone cliffs in the park (Nekola, *unpublished data*). Unfortunately, verification of Levi & Levi's specimens was not possible as their repository is unknown.

Shell Morphology

As only roughly a dozen shells had been previously collected (Oughton, 1948; Pilsbry, 1948; Dawley, 1955), the 112 adult individuals secured in these analyses (Table 1) represent the first time a series of *Vertigo nylanderi* has been available. These shells ranged from 1.3-1.8 mm in height and 0.75-1.0 mm in width. Thus, some individuals were both shorter and more narrow than the previously published size range (1.55-1.8 mm tall, 0.9-1.0 mm wide; Pilsbry 1948).

The shape and appearance of these specimens (Fig. 2i-1) agree well with the descriptions and figure from Pilsbry (1948). In particular, the width of the body and penultimate whorls are similar; the outer margin of the aperture has a strong sinulus; a strong angular lamella exists in the aperture; the basal lamella is weak; and the lower palatal lamella is very deeply inserted, with its outer edge coincident with the inner end of the upper palatal. A deep, groove-like indentation on the outside of the shell over the lower palatal lamella is also present. However, unlike the description from Pilsbry (1948) few (if any) shells were noted to be of a cinnamon color, with most being a much lighter shade of yellow-brown.

As noted by Sterki (Pilsbry, 1948), the deeper insertion of the lower palatal lamella as compared to the upper, and the depression on the outside of the shell over the

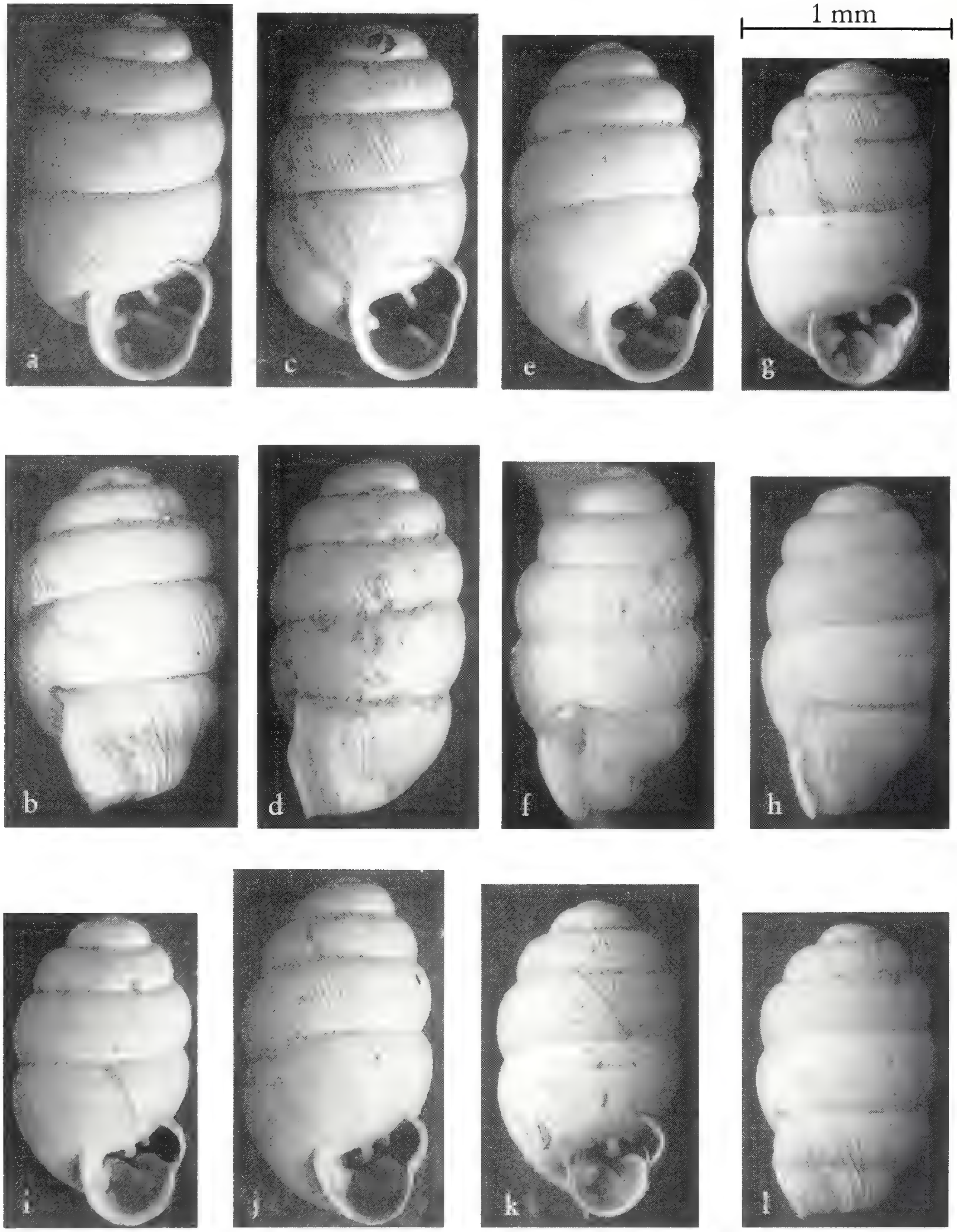

Fig. 2. Scanning electron micrographs of *Vertigo nylanderi* and related taxa. **a,b.** *V. hubrichti*, Benderville Wayside, Brown County, Wisconsin, USA (87° 50'31" W, 44° 36'47" N), UWGB Collection #644. **c.** *V. paradoxa*, Maple Hill, Chippewa County, Michigan, USA (84° 46'55" W, 46° 9'34" N), #2270. **d.** *V. paradoxa*, Scott Quarry, Chippewa County, Michigan, USA (84° 50'4" W, 46° 10'43" N), #3292. **e, f.** *Vertigo* n.sp. *sensu* Frest (1991), Iron Fence Wayside, Brown County, Wisconsin, USA (87° 49'40" W, 44° 37'14" N), #1684. **g, h.** *V. arthuri*, Two Rivers State Natural Area, Roseau County, Minnesota, USA (96° 20'42" W, 48° 39'21" N), #5223. **i.** *V. nylanderi*, Garden Corners, Delta County, Michigan, USA (86° 32'4" W, 45° 53'23" N), #2967. **j.** *V. nylanderi*, Corbisier Farm, Door County, Wisconsin, USA (87° 32'57" W, 44° 45'17" N), #5057. **k.** *V. nylanderi*, Iron Springs State Natural Area, Clearwater County, Minnesota, USA (95° 15'5" W,47° 15'11" N), #5779. **l.** *V. nylanderi*, Kiel Marsh, Calumet County, Wisconsin, USA (88° 3'34" W, 43° 53'52" N), #4538. Micrographs were taken with a Hitachi S-2460N Scanning Electron Microscope in N-SEM Mode (10 Pa; 22 kV) with a backscatter detector and #2 Gamma Correction.

palatals, suggests closer affinity of *Vertigo nylanderi* to *V. paradoxa* and *V. hubrichti* than other eastern North American *Vertigo*. Comparisons can also be drawn with a putative, undescribed, new taxon which (if valid) is closely related to *V. hubrichti* (Frest, 1991). *V. nylanderi* can be distinguished from these taxa (Fig. 2a-f) because it possesses a columellar lamella of greater volume than the parietal, a strong angular lamella, a very weak basal lamella, and a very deeply set lower palatal. This last feature is most easily seen by looking at the outside of the shell with the aperture facing down. In *V. nylanderi*, the lower palatal is so deeply set that the depression over it runs parallel to the aperture on the very back of the shell. In *V. paradoxa* and *V. hubrichti* the less deep insertion of the lower palatal places this depression at an acute angle from the aperture on the side of the shell.

While individuals intermediate between *Vertigo nylanderi* and *V. paradoxa* do not exist (even at sites of co-occurrence), some slightly intermediate individuals between *V. nylanderi* and *V. hubrichti* were located at the Corbisier Farm site. These were the tallest shells encountered (1.7-1.8 mm), had the strongest basal lamellae, and had a columellar lamella only slightly larger in volume as compared to the parietal. However, in all other regards these individuals appeared identical to other *V. nylanderi* specimens. These differences in shell morphology at the Corbisier Farm are likely due to ecotypic variation rather than to genetic introgression, as these were the only individuals not found in a wetland environment.

Vertigo nylanderi also bears some resemblance to *V. arthuri* by possessing an angular lamella, a columellar lamella of greater volume as compared to the parietal, and a lower palatal lamella more deeply set as compared to the upper. However, *V. arthuri* is easily distinguished from *V. nylanderi* by having a thickened callus adjacent to the palatal lamellae, a less deeply inserted and shorter lower palatal lamella, and a distinct crest in back of the aperture (Fig. 2g-h).

Habitat Preferences

Except for the Corbisier Farm, *Vertigo nylanderi* was limited to wooded wetlands. Tamarack (*Larix laracina* (DuRoi) K.Koch) and/or Black Ash (*Fraxinus nugra* Marsh.) were usually present, and either (or both) of these species dominated the tree canopy tree at all but three sites. At Townhall Road and Tisch Mills 2, White Cedar (*Thuja occidentalis* L.) was the dominant tree. At Lily Lake 2, White Cedar, Yellow Birch (*Betula lutea* Mich.), and Hemlock (*Tsuga canadensis* (L.) Carr.) were co-dominant. All sites had a ground layer harboring nutrient-rich wetland bryophytes (e.g. *Cratoneuron filicinum* (Hedw.) Spruce, *Mnium cuspidatum* Hedw., *M. punctatum* Hedw., *Thuidium delicatulum* (Hedw.) BSG), various sedges (e.g. *Carex lacustris* Willd., *C. leptalea* Wahlenb.) and small shrubs (e.g. *Ribes lacustris* (Pers.) Poiret and *Rhamnus alnifolia* L'Her). *Sphagnum* mosses were generally rare or absent. Some of the Minnesota sites are also known to harbor *Malaxis paludosa* (L.) Sw., one of North America's rarest boreal orchids.

The Corbisier Farm population was found in a very different situation: a White Cedar grove growing on top of an anthropogenic stone pile. According to the Corbisier family, this stone pile dates back almost 100 years. Although seemingly very different, some similarities were noted between this and other *Vertigo nylanderi* sites. First, the stone pile was constructed on top of a spring next to a cold stream, which makes its soil cool and wet. Second, the stone pile rests within a wetland matrix, which before agricultural conversion was likely dominated by White Cedar, Tamarack, and Black Ash. The history and ecological conditions of the Corbisier Farm stone pile appear unique, as none of the other anthropogenic stone piles in the region which have been analyzed support *V. nylanderi* or other species (e.g. *Euconulus alderi, V. bollesiana*) which occur here.

Associated Species

A total of 54 terrestrial gastropod taxa were sympatric with *Vertigo nylanderi* (Table 2). Twelve of these (*Carychium exiguum, Nesovitrea electrina, Euconulus alderi, Striatura milium, Zonitoides arboreus, Gastrocopta tappaniana, Striatura exigua, Strobilops labyrinthica, Vertigo elatior, Punctum minutissimum, Carychium exile*, and *Columella simplex*; 22% of total) were found in 50% or more of sites. Of the remaining, 36 (over 66% of the total) taxa were found in less than 25% of sites.

Two general associations were noted. Tamarack-dominated sites in eastern Wisconsin and northern Michigan (Angling Swamp, Birch Creek, East River Road, Garden Corners, Lily Lake County Park 1, Maxton Plains Center 2, Prentiss Bay, Tisch Mills 1, Toft Point) supported a very consistent fauna essentially limited to the nine most common taxa. Average species richness of these sites is 11.9. Tamarack-dominated sites in Minnesota (Bowstring, Iron Springs) had a similar, though richer, fauna (16-18 species). These associates are consistent with those listed by Oughton (1948) for the 3 Ontario sites. Olaf Nylander also collected *Vertigo elatior* from the type station (Pilsbry, 1948).

Black Ash, White Cedar, and/or Alder dominated sites (Bear Paw Point E, Bear Paw Point W, Corbisier Farm, Keil Marsh, Lily Lake 2, Morgan Marsh, Pennington Bog, Reforestation Camp, Tisch Mills 2, Townhall Road, Zander Road) were found to harbor not only the common

Table 2. Species associated with *Vertigo nylanderi* in Michigan, Minnesota, and Wisconsin. Nomenclature is based on Hubricht (1985).

Species	Site																						Total
	Michigan						Minnesota					Wisconsin											
	1	2	3	4	5	6	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10	11	
Carychium exiguum (Say, 1822)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	22
Nesovitrea electrina (Gould, 1841)	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	21
Euconulus alderi (Gray, 1840)	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x			x	19
Striatura milium (Morse, 1859)		x	x	x	x	x	x	x	x	x	x	x	x	x		x		x	x	x	x	x	19
Zonitoides arboreus (Say, 1816)	x	x	x		x	x	x	x	x	x	x		x	x	x	x	x	x	x		x	x	19
Gastrocopta tappaniana (C. B. Adams, 1842)	x	x	x	x			x	x	x	x	x	x		x	x	x	x	x	x		x	x	18
Striatura exigua (Stimpson, 1847)	x		x	x	x		x	x	x	x	x	x	x	x				x	x	x	x	x	17
Strobilops labyrinthica (Say, 1817)	x		x	x	x		x	x	x	x	x		x	x		x		x	x	x	x	x	17
Vertigo elatior Sterki, 1894	x	x	x	x	x	x	x	x	x	x	x	x		x		x		x			x	x	17
Punctum minutissimum (I. Lea, 1841)	x	x		x	x	x	x	x	x	x	x	x	x							x			13
Carychium exile H. C. Lea, 1842					x	x	x		x	x	x		x	x					x	x	x		11
Columella simplex (Gould, 1841)		x		x	x	x	x	x		x	x		x					x			x		11
Deroceras laeve (Müller, 1774)				x				x		x		x				x			x		x		7
Gastrocopta contracta (Say, 1822)									x	x			x	x		x	x				x		7
Helicodiscus parallelus (Say, 1817)									x	x						x	x		x		x	x	7
Helicodiscus shimeki Hubricht, 1962					x						x		x	x		x				x	x		7
Discus catskillensis (Pilsbry, 1898)					x	x	x			x	x										x		6
Discus cronkhitei (Newcomb, 1865)				x			x	x	x							x	x						6
Gastrocopta pentodon (Say, 1821)										x			x	x		x					x		5
Hawaiia minuscula (A. Binney, 1840)									x	x						x	x					x	5
Catinella avara (Say, 1824)								x		x					x	x							4
Cochlicopa lubrica (Müller, 1774)									x		x					x	x						4
Euconulus fulvus (Müller, 1774)													x	x			x				x		4
Nesovitrea binneyana (Morse, 1864)					x		x			x	x												4
Punctum vitreum H. B. Baker, 1930														x		x	x				x		4
Striatura ferrea Morse, 1864					x								x								x	x	4
Vertigo gouldi (A. Binney, 1843)					x								x			x					x		4
Vertigo milium (Gould, 1840)														x			x				x	x	4
Vertigo ovata Say, 1822								x	x						x							x	4
Cochlicopa lubricella (Porro, 1838)									x	x							x						3
Euconulus polygyratus (Pilsbry, 1899)					x								x								x		3
Glyphyalinia indentata (Say, 1823)			x											x								x	3
Punctum n. sp.										x					x	x							3
Stenotrema leai leai (A. Binney)															x		x					x	3
Succinea ovalis Say, 1817				x											x	x							3
Vallonia pulchella (Müller, 1774)							x										x					x	3
Vertigo bollesiana (Morse, 1865)																x	x				x		3
Vertigo cristata (Sterki, 1919)							x			x	x												3
Zonitoides nitidus (Müller, 1774)												x				x	x						3
Anguispira alternata (Say, 1817)					x												x						2
Gastrocopta holzingeri (Sterki, 1889)													x									x	2
Haplotrema concavum (Say, 1821)													x								x		2
Hendersonia occulta (Say, 1831)													x								x		2
Oxyloma retusa (I. Lea, 1834)									x													x	2
Strobilops affinis Pilsbry, 1893														x		x							2
Vallonia gracilicosta Reinhardt, 1883							x			x													2
Vertigo arthuri (von Martens, 1884)							x		x														2
Vertigo paradoxa Sterki, 1900			x				x																2
Planogyra asteriscus (Morse, 1857)					x																		1
Pupilla muscorum (Linné, 1758)					x																		1
Stenotrema fraternum fraternum (Say, 1824)					x																		1
Vallonia costata (Müller, 1774)																	x						1
Vertigo pygmaea (Draparnaud, 1801)																						x	1
Vitrina limpida Gould, 1850																	x						1
Immature *Cochlicopa*																					x		
Immature *Discus*		x																					
Immature Polygyrinae												x		x									
Immature Succineidae												x									x		
Immature *Vallonia*			x		x																		
Total Richness (including *V. nylanderi*)	8	13	11	14	22	13	21	16	21	25	18	13	20	20	12	24	22	11	12	9	28	21	

Site Code Legend for Table 2:

Michigan:
1. Maxton Plains Center 2
2. Prentiss Bay
3. Garden Corners
4. Angling Swamp
5. Townhall Road
6. Birch Creek

Minnesota:
1. Pennington Bog
2. Iron Springs
3. Bear Paw Point W
4. Bear Paw Point E
5. Bowstring

Wisconsin:
1. Lily Lake Tamarack
2. Lily Lake White Cedar
3. Reforestation Camp
4. East River Road
5. Kiel Marsh
6. Corbisier Farm
7. Toft Point
8. Tisch Mills 1
9. Tisch Mills 2
10. Zander Road
11. Morgan Marsh

associates, but the bulk of the rarer ones as well. Most of these additional species are characteristic of mesic, calcareous woodlands. The Morgan Marsh site is located along a road, and a number of the additional species found there are typical of disturbed situations (e.g. *Vallonia pulchella, Vertigo pygmaea*). Species richness of these sites was also considerably higher, with a mean of 22.4 being observed. Minimum richness never fell below 20, with a maximum of 28 being recorded from a ca. 100 m^2 area at Zander Road. These sites represent the richest land snail communities not associated with carbonate bedrock outcrops in the region.

Pleistocene History

Vertigo nylanderi has been identified from 20,000 B.P. (Frest 1991) and 750,000 B.P. (Miller *et al.*, 1994) deposits in Illinois. During the late Pleistocene, nutrient-rich wetlands of Tamarack and Black Ash (Miller, 1980; Baker *et al.,* 1996; Jackson *et. al.*, 1997) were common in the landscape. Regional climates of this period were also less extreme than today, having similar winter temperatures, but cooler summers and more constant precipitation (Prior, 1991). Roughly similar climatic conditions persist in modern Tamarack and Black Ash dominated wetlands, especially those along the shores of Lakes Huron and Michigan where the buffering effect of lake waters lowers summer temperatures, creates warmer winter temperatures, and allows for more constant precipitation than is otherwise present in the continental interior (Curtis, 1959; Eichenlaub, 1979). Tamarack and Black-Ash wetlands in the western Great Lakes could thus represent close edaphic and microclimatic analogues to Pleistocene wetland habitats. Given the almost complete limitation of modern *V. nylanderi* to such sites, it could be best to consider this species a glacial relict. A similar argument has been advanced by Miller (1980, 1987) to suggest that disjunct populations of western calciphile plant species in the northeastern U.S. and southeastern Canada represent glacial relicts.

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Identity of the Land Snail *Monadenia rotifer* Berry, 1940 (Gastropoda: Pulmonata: Bradybaenidae)

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Abstract: *Monadenia rotifer*, described from a single worn and empty shell and not subsequently recognized in living populations, is a synonym of *Monadenia marmarotis*, found in neighboring parts of the Marble Mountains, Siskiyou County, California. The holotype of *M. rotifer* is an unusually coarsely sculptured specimen of *M. marmarotis*.

Key Words: land snail, California, systematics, synonymy

Berry (1940) described five new species and four new subspecies of the land snail genus *Monadenia* Pilsbry, 1895, from northern California. I reviewed their status recently in connection with recent sampling in the Klamath Mountains and preparation of a manual on the land mollusks of California. The new taxa were illustrated originally with camera lucida line drawings. The descriptions were based almost entirely on shell characters. Except for a few notes on the external appearance of living snails, no anatomical information was presented. These taxa have remained somewhat obscure in the literature. Pilsbry (1948: 1092-1093) noted their existence but did not republish their descriptions as he did with other taxa described while his monograph was in preparation. They were omitted from Smith's (1970) tabulation of rare and endangered western land snails. The first edition of the American Fisheries Society's list of the common names of aquatic invertebrates (Turgeon *et al.*, 1988) unaccountably cited the species as "classification uncertain". (The second edition of the list [Turgeon *et al.*, 1998] removed that designation.) Nevertheless, biologists actually working with the taxa generally have had no trouble recognizing them (Roth, 1981; Roth and Pressley, 1986), and their obscurity is largely undeserved.

Monadenia rotifer Berry, 1940, is a probable exception. It was described from a single imperfect, bleached shell. Berry's description emphasized the angulate periphery and the presence of rib-like ridges, particularly on the upper surface of the shell. Practically all other characters can be duplicated in material now at hand of *Monadenia marmarotis* Berry, 1940, from neighboring parts of the Marble Mountains, Siskiyou County. The degree of angulation and ribbing in *M. marmarotis* is variable. After examination of the holotype of *M. rotifer* (herein illustrated by photographs for the first time), I have concluded that it is an aberrant specimen of *M. marmarotis*.

The following abbreviations are used: BR, author's collection, San Francisco, California; CAS, California Academy of Sciences; SBMNH, Santa Barbara Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution. Whorls are counted by the method of Pilsbry (1939: xi, fig. B).

SYSTEMATICS

Bradybaenidae Pilsbry, 1939

Monadenia Pilsbry, 1895

Type-species: *Helix fidelis* Gray, 1834; by original designation.

Monadenia marmarotis Berry, 1940

(Figures 1-8)

Monadenia marmarotis Berry, 1940: 3-5, figs. 1, 2. —Turgeon *et al.*, 1998: 155, 300.

Monadenia marmoratis [*sic*] Berry, Pilsbry, 1948: 1092 (spelling error). —Ingram, 1949: 31. —Turgeon *et al.*, 1988: 144.

Monadenia rotifer Berry, 1940: 5-6, figs. 3, 4. Pilsbry,

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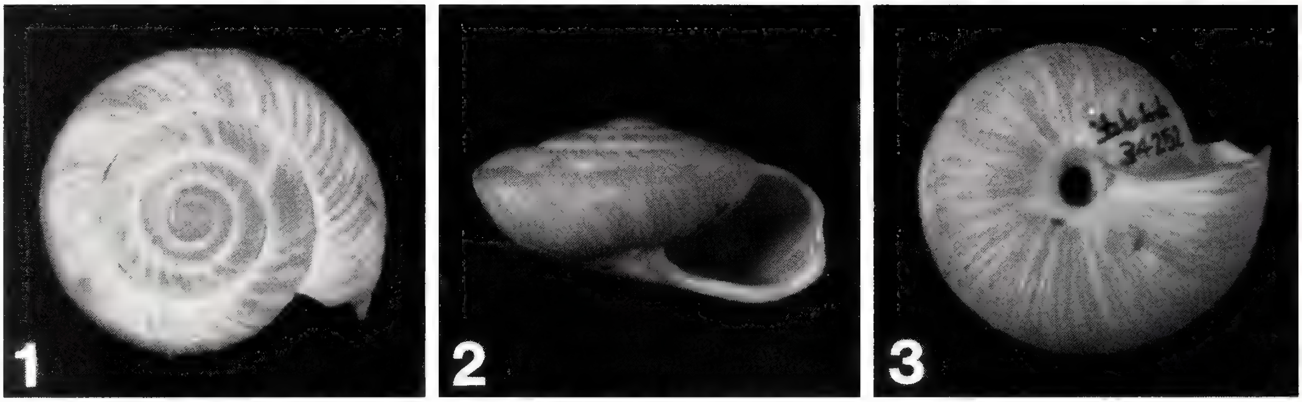


Figs. 1-3. Holotype of *Monadenia rotifer* Berry, 1940, SBMNH 34252, top, apertural, and basal views. Diameter 22 mm.

1948: 1092. —Ingram, 1949: 31-32. —Turgeon *et al.*, 1998: 155, 300.

Monadenia rotifera Berry, Turgeon *et al.*, 1988: 144 (unjustified emendation).

Description. Shell 18.4-24.6 mm in diameter, solid, depressed, with 5.1-6.1 whorls. Spire low, its sides nearly straight; suture moderately to strongly impressed; early whorls well-rounded, later ones flattened. Periphery obtusely angulate above middle of whorl. Embryonic whorls 1.8-2.0, nuclear tip smooth, followed by very fine granulation tending to fuse into radial wrinkles on first whorl, thereafter aligning more or less in diagonal series. Post-embryonic sculpture of coarse but low, irregular, collabral rugae; apertural side of rugae sloping gently, abapertural side steeper, sometimes overhanging; fine, incised striae sometimes present on shoulder and base, much interrupted by growth rugae. Aperture broadly ear-shaped, oblique. Lip turned outward, reflected, and thickened by callus. Inner lip impinging slightly on umbilicus. Umbilicus contained 6.3-9 times in diameter. Ground color white or pale yellow; spire and shoulder orange-brown to chestnut, usually with darker radial streaks. Peripheral band strong, blackish brown; light zone above peripheral band faint. Base chestnut brown. Periostracum smooth, sometimes with oily luster. Anatomy unknown.

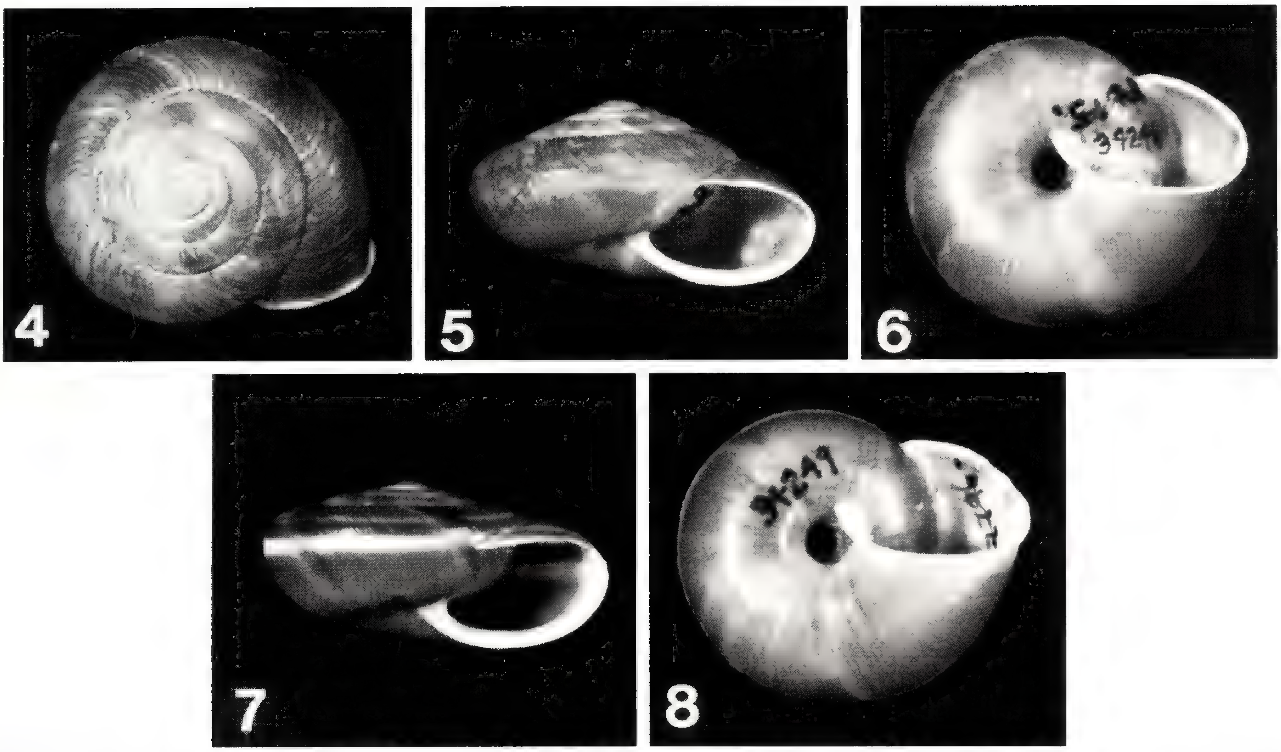
Type material. *Monadenia marmarotis*: Holotype, SBMNH 34248 (shell), CALIFORNIA: Siskiyou County: "Alt. ca. 5900 ft., one-quarter to one-half mile south of Marble Valley Ranger Station, Marble Valley"; L. Shapovalov coll. 22 July 1934. Paratypes, from same locality as holotype (BR 1026 [4 specimens], BR 1777 [3], CAS 064389 [4], CAS 065630 [8], CAS 065631 [6], SBMNH 34249 [31], SBMNH 34250 [10], SBMNH 34251 [44], USNM 522578 [4]).

Monadenia rotifer: Holotype, SBMNH 34252 (shell), CALIFORNIA: Siskiyou County: "Alt. ca. 6,000 ft., on trail one-half mile west of Whiskey [*sic*; = Whisky] Camp, Salmon Mountains"; A. C. Taft coll. 17 July 1934.

Referred material of *M. marmarotis*. CALIFORNIA: Siskiyou County: Marble Mountain, above Marble Valley, elev. 2000 m, J. Williams coll. 22 July 1934 (SBMNH 107795 [3 specimens]); Kelsey Creek Trail, 1.7 km below Marble Valley Ranger Station, L. Shapovalov coll. 23 July 1934 (SBMNH 108618 [2]); Marble Valley, under loose pieces of marble, D. V. Hemphill coll. 5 November 1976 (BR 848 [4]); Skunk Hollow Cave, 24 km W of Fort Jones, D. C. Rudolph, D. Cowan, B. Van Ingen coll. 29 April 1979 (BR 1193 [22]); Planetary Dairy Cave, Marble Mountain Wilderness, D. C. Rudolph, D. Cowan, B. Van Ingen coll. 29 April 1979 (BR 1194 [3]); Trail Junction Cave, Marble Mountain Wilderness, D. C. Rudolph, D. Cowan, B. Van Ingen coll. 29 April 1979 (BR 1305 [2]); Marble Mountain Cave, elev. 6800 ft [2100 m], M. K. Gausen coll. July 1998 (BR 2171 [2]).

Comparisons. In general shell characters, the holotype of *Monadenia rotifer* (Figures 1-3) and *M. marmarotis* (Figures 4-8) are much alike. Both show a solid, depressed shell with a low, nearly straight-sided spire and weakly impressed sutures. The apex of *M. marmarotis* is often mamillate, with projecting embryonic whorls, as it is in the holotype of *M. rotifer*. After a smooth nuclear tip, the embryonic whorls of *M. marmarotis* are sculptured with very fine granulation tending to fuse into radial wrinkles on the first whorl, thereafter aligning more or less in diagonal series. The embryonic whorls of *M. rotifer* are worn, but the original sculpture apparently consisted of fine granulation tending to align in diagonal series.

The diameter of the holotype of *Monadenia rotifer*, slightly more than 22 mm (complete original diameter unknown because of slight damage to the outer lip), and the number of whorls, 5.1, are within the range known for *M. marmarotis*. The umbilicus is contained about 8.8 times within the shell diameter, likewise within the range shown by *M. marmarotis*. The inner lip scarcely impinges on the umbilicus.



Figs. 4-8. *Monadenia marmarotis* Berry, 1940. 4-6, holotype, SBMNH 34248, top, apertural, and basal views. Diameter 22.5 mm. 7, 8, paratype, SBMNH 34249, apertural and basal views. Diameter 22.5 mm.

The original shell color of *Monadenia rotifer* is unknown because the holotype is a bleached "bone." The only color remaining is a pale orange trace of the peripheral band. This is consistent with shell coloration in *M. marmarotis*, in which the peripheral band is darker than either the basal patch or the shoulder of the whorl and is the last color to fade out in old shells.

In *Monadenia rotifer* the periphery is angulate above the middle of the whorl (Figure 2). The angulation persists to the aperture. The shells of all *Monadenia* species begin growth with an angular periphery (compare Roth, 1981: figs. 9a-9c); in most taxa the profile grades toward broadly rounded as maturity is reached. In *M. marmarotis* the periphery is angular until approximately the last 0.33-0.25 whorl. The location of the angulation with respect to the middle of the whorl varies, but a high angulation occurs in many specimens, including a paratype (Figure 7).

The post-embryonic sculpture of *Monadenia rotifer* consists of coarse, collabral rugae, strong on the shoulder of later whorls and fading out on the base. The rugae are convex on the apertural side, concave on the abapertural side. They are not as distinct and rib-like as Berry's (1940) comparison to *Monadenia circumcarinata* (Stearns, 1879) might suggest. Instead, they seem merely to be a strong version of the rugose collabral sculpture present to a greater or lesser extent on the top surface of *M. marmarotis* shells (Figure 4). The rugae on *M. rotifer* are visually emphasized by erosion, which has removed the chalky surface shell layer from their crests but left it present in the interspaces (Figure 1).

Additional remarks. Whisky Camp is located at 41°33'14" N, 123°13'51" W. The type locality of *Monadenia rotifer*, on the trail 0.8 km west of Whisky Camp, is in NW1/4 sec. 28, T. 43 N, R. 12 W, Mt. Diablo Base and Meridian (USGS Marble Mountain Quadrangle, 7.5 minute series, 1983 ed.). The type locality of *M. marmarotis* is in SW1/4 sec. 23, T. 43 N, R. 12 W, within 4 km of the type locality of *M. rotifer* and at approximately the same elevation. The other known localities for *M. marmarotis* are in the same vicinity, and some are at least as close to the *M. rotifer* locality. (In keeping with speleological practice, the named caves are not more precisely located here.)

Empty shells are found in both forested areas (western white pine, Shasta red fir, foxtail pine) and relatively open areas with little vegetation. All localities appear to be on a single tectonic block of white or gray-and-white laminated marble of possible Paleozoic age (Donato *et al.*, 1982; Donato and Hale, 1984).

The conclusion of this study could be further tested by the finding of a living population having the characteristics of the holotype of *Monadenia rotifer*. Particularly persuasive would be findings that the reproductive systems of such snails differed from those of *M. marmarotis* from Marble Valley.

Because both names *Monadenia marmarotis* and *Monadenia rotifer* were proposed simultaneously in the same publication, in choosing the former as the valid name I am acting as a First Reviser in the sense of ICZN Article 24.2. I have selected *Monadenia marmarotis* as the valid name because it is based on a more extensive type lot (with characters confirmed by subsequent sampling) whereas *M. rotifer* is based on a single, apparently aberrant specimen.

Turgeon *et al*.'s (1988) citation of the name as *"Monadenia rotifera"* was an unjustified emendation based on the assumption that the specific epithet is an adjective. The specific name is a noun in apposition (*rotifer*, a wheel-bearer) and does not change termination to agree in gender with the genus.

ACKNOWLEDGMENTS

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Aegopinella nitidula (Draparnaud, 1805) (Gastropoda: Zonitidae) in British Columbia – first confirmed North American record

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Abstract: The European land snail, *Aegopinella nitidula* (Draparnaud, 1805), is reported for the first time from British Columbia, from three sites in the city of Vancouver. These new records are the only documentation of the species in North America, except for two old records that are probably erroneous and have been ignored in recent literature. Comparisons are made between *A. nitidula* and similar native and introduced species. Information about its ecology in Europe is summarized.

Key Words: introduced land snails, Pulmonata, Vancouver, Canada

Many species of European terrestrial snails and slugs have proven particularly well suited for introduction by humans to other parts of the world, and in North America 45 species are introduced and apparently established (compiled from Turgeon *et al.*, 1998; Forsyth, 1999; Reise *et al.*, 2000; and this paper). In general, these species tend to be synanthropic and opportunistic. Most of the slugs and some of the larger snails are important economically because of damage that they inflict upon crops. Also of great concern is the potential long-term impact that carnivorous species may have on native fauna. Frest & Rhodes (1982), for example, suggested a connection between the predatory snail *Oxychilus draparnaudi* (Beck, 1837) and a reduction in a local population of native snails in Iowa. The New World predatory snail *Euglandina rosea* (Férussac, 1818) has certainly caused the extinction of several snails endemic to Pacific islands (Civeyrel and Simberloff, 1996).

The land snails and slugs of British Columbia have historically been neglected, and introduced species in particular have been poorly documented (but see Rollo and Wellington, 1975). Recently Forsyth (1999) updated the published record of nine exotic land snails in the province, and Reise *et al.* (2000) reported the first known North American records of the worm slug, *Boettgerilla pallens* Simroth, 1912 from near Victoria, British Columbia. The present paper reports for the first time the European zonitid *Aegopinella nitidula* (Draparnaud, 1805) from three sites in Vancouver, British Columbia, and confirms the existence of this species in North America (Fig. 1). It seems likely that old records of this species from California and Great Slave Lake, Northwest Territories (Dall, 1905; Pilsbry, 1946) were erroneous, as discussed below.

MATERIALS AND METHODS

RGF has made extensive collections of land snails from 80 sites in the urban areas of Vancouver and Victoria (Forsyth, 1999) and from more than 400 sites throughout British Columbia, mostly since 1995. In addition JMCH and HR spent two weeks in July 1998 collecting land mollusks in southern British Columbia, paying particular attention to synanthropic habitats. Specimens were collected by hand from under wood, logs, rocks and leaf litter. Most material was preserved in 70% ethanol and specimens are deposited in the Royal British Columbia Museum (RBCM), Victoria, B. C., or the Staatliches Museum für Naturkunde Görlitz (SMNG), Görlitz, Germany. Additional material is in the private collection of RGF. Our determination of *Aegopinella nitidula* was based on comparison of shell and anatomical characters with European specimens and was confirmed by A. Riedel (Warsaw).

RECORDS OF *AEGOPINELLA NITIDULA* IN VANCOUVER

Aegopinella nitidula was found at only three localities, all in the city of Vancouver:

Path at north end of Blanca Street, Vancouver, B.C.

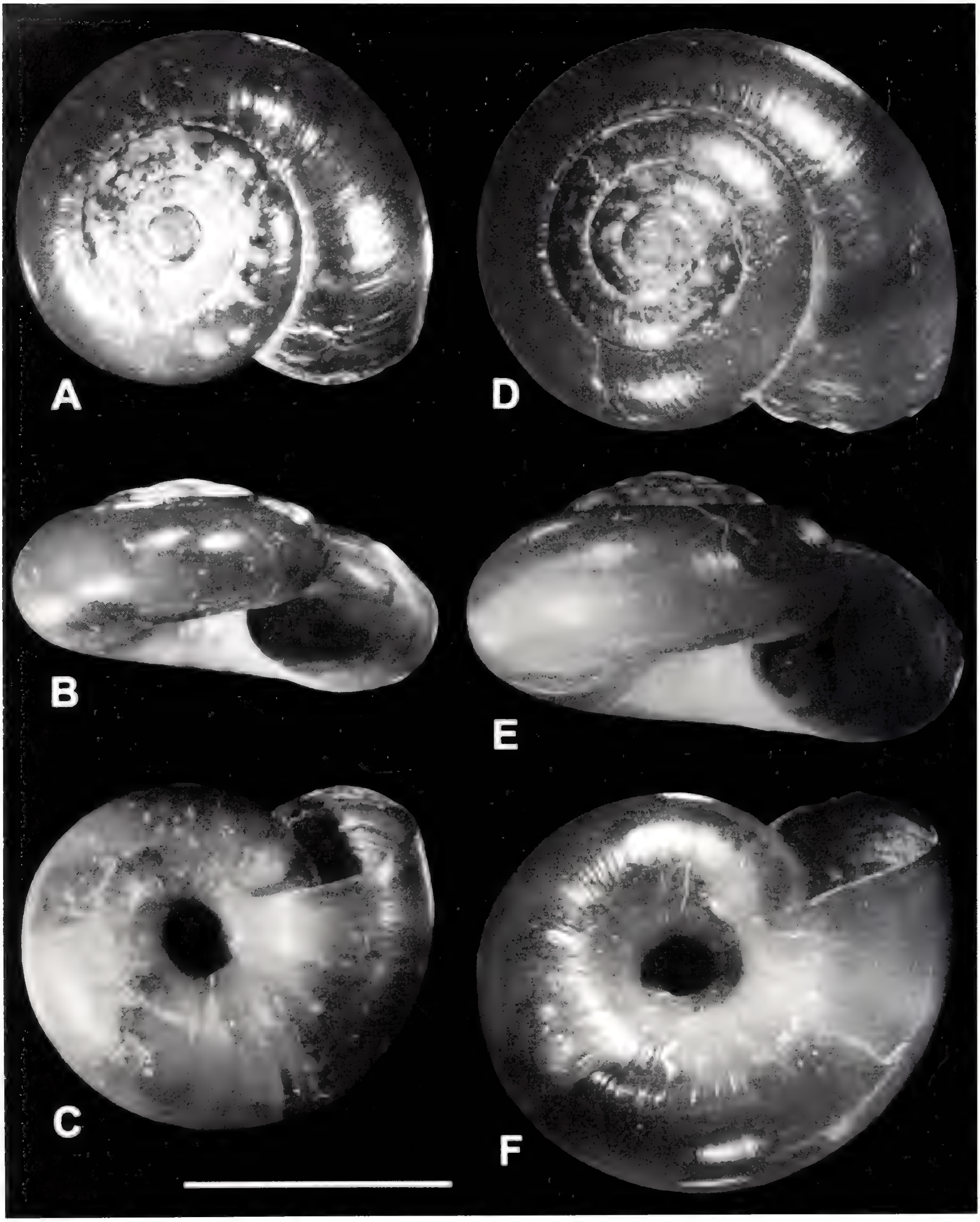

Fig. 1. *Aegopinella nitidula* (Draparnaud, 1805). A-C. Specimen from Stanley Park, Vancouver, British Columbia, Canada; 17 July 1998 (SMNG p5982). D-F. Specimen from Leigh Delamere motorway services, Wiltshire, England; 19 April 2000 (SMNG p8023). Scale bar = 5 mm.

(49°16.5'N, 123°12.8'W). RGF, collector. 24 November 1997. Forsyth Collection, 1 specimen, dry.

Ibid., T. J. Forsyth and RGF, collectors. 30 December 1998. RBCM 999-00029-002, 6 specimens, 70% ethanol.

Vicinity of the park drive at 33rd Avenue, Queen Elizabeth Park, Vancouver, B.C. (49°14.5'N, 123°06.9'W). HR and JMCH, collectors. 18 July 1998. SMNG p5981, 12 specimens, 70% ethanol.

Vicinity of Stanley Park Drive and Lagoon Drive, between road and golf course, west of Lost Lagoon, Stanley Park, Vancouver, B.C. (49°17.6'N, 123°08.7'W). HR and JMCH, collectors. 17 July 1998. SMNG p5982, 32 specimens, 70% ethanol.

At the Blanca Street site, *Aegopinella nitidula* was found in association with five other species of gastropods: *Deroceras reticulatum* (Müller, 1774); *Arion hortensis* complex Férussac, 1819; *Lauria cylindracea* (da Costa, 1778); *Oxychilus draparnaudi* (Beck, 1837); and *Cochlicopa lubrica* (Müller, 1774). The site was at the end of a road in a residential neighborhood adjacent to a wooded bank. At the top of the bank, in the area where specimens were found, plants were mostly exotic ornamentals mixed with some native trees and shrubs. Regular dumping of garden waste was apparent and most specimens were found on the ground under leaf material and brush.

In Stanley Park *Aegopinella nitidula* was common in flower beds and under planted shrubs in a more cultivated part of the park. *A. nitidula* was associated with *Cochlicopa lubrica; Oxychilus alliarius* (J. S. Miller, 1822); *Arion subfuscus* (Draparnaud, 1805); *Arion hortensis* complex; *Limax maximus* Linnaeus, 1758; *Deroceras reticulatum*; and *D. panormitanum* (Lessona and Pollonera, 1882).

The habitat of *Aegopinella nitidula* in Queen Elizabeth Park was very similar to where we found the species in Stanley Park. Associated mollusks were *Cochlicopa lubrica; Lauria cylindracea; Arion subfuscus; A. distinctus* Mabille, 1868; and *Vitrea contracta* (Westerlund, 1871).

Although Forsyth (1999) has made extensive collections of land snails in similar habitats elsewhere in British Columbia, *Aegopinella nitidula* was collected only at these three sites within the city of Vancouver. Associated terrestrial mollusks are all ultimately of European origin, except for *Cochlicopa lubrica*, a native, Holarctic snail with a strong tendency to be synanthropic (Roth and Pearce, 1984). In Europe *A. nitidula* is often in habitats disturbed by human activities (Kerney and Cameron, 1979) and, therefore, is a prime candidate for foreign introduction. Rollo and Wellington (1975) and Forsyth (1999) suggested that the movement of garden waste from one site to another is very important in the spread of terrestrial slugs and snails in urban areas. The paucity of records for this species relative to certain other exotic land snails and slugs (see Forsyth, 1999; Rollo and Wellington, 1975) perhaps suggests a more recent introduction.

DISTRIBUTION AND ECOLOGY IN EUROPE

Aegopinella nitidula is native to Europe, with a northwestern distribution (Kerney *et al.*, 1983; Riedel, 1970). The most northern records are along the Atlantic coast of Norway, and it occurs as far south as Spain. The slanting southeastern border to its distribution keeps mostly north of such mountain ranges as the Carpathians, Alps, Juras, and Pyrenees as well as north of the Mediterranean region.

Aegopinella nitidula is catholic in its habitats, found under leaf-litter in coniferous and deciduous woodland, damper grassland, river banks, the base of rocks and walls, hedgerows, waste ground and gardens (Kerney and Cameron, 1979). It is tolerant of a wide range of soil pH (even pH = 4.8, Hermida *et al.*, 1995). Within parts of Europe *A. nitidula* is encountered frequently and can occur at quite high densities (e.g. average densities of 8, 14, 16 and 18 per m^2 in different woodlands – Mason, 1970; Mordan, 1977; Cameron, 1982; Corsmann, 1990).

Two studies in British woodlands have found a biennial life cycle in this species (Mordan, 1978; Cameron, 1982). The numbers of the smallest juveniles peaked in autumn at one site, but the peak started earlier at the other site, and continued into late winter at a site in Germany (Corsmann, 1990). In Mordan's population, snails became sexually mature by December of their second year, dying off the following summer or autumn. Egg numbers peaked in summer but some were recorded in most months.

Fecal analysis indicated that most of the diet is dead plant material, but 10% of faces contained some molluscan tissue (Mordan, 1977). Behavioral observations have confirmed that *Aegopinella nitidula* preys on other snails up to 4.5 mm in diameter and slugs up to 17 mm long (Frömming, 1954; Mordan, 1977). They attack other zonitid snails initially through the shell aperture, but obtain further flesh by later drilling a hole through the shell, usually from the underside (Mordan, 1977). Circumstantial evidence suggests that predation by *A. nitidula* might even affect the density and distribution of other snail species (Mordan, 1977). Its introduction to North America could, therefore, have repercussions on the native mollusk fauna. Earthworms and Enchytraeidae are also readily depredated by *A. nitidula*, at least in captivity (Frömming, 1954).

SIMILAR SPECIES AND THE IDENTIFICATION OF *AEGOPINELLA NITIDULA*

The shells of zonitids are in general thin, more or less glossy and often somewhat translucent. The aperture lacks denticles and the outer lip is unthickened. *Aegopinella nitidula* has a thin, light yellowish-brown shell having a distinctive waxy appearance. Fully grown shells measure 8-10 mm in diameter and have roughly $4^1/_2$ whorls (Kerney and Cameron, 1979). Under a high magnification fine spiral incised lines and incremental lines are evident on the shell's surface. The width of the umbilicus is approximately 20-25% that of the shell. Around the umbilicus, the shell is more opaque than elsewhere and distinctly whitish (Fig. 1). The animal is dark gray with a slight bluish tinge on top, with paler flanks and tail, and a pale sole.

In Europe there are many *Aegopinella* species similar in external appearance to *A. nitidula*. In most cases dissection is necessary for species identification (Riedel, 1957, 1983; Forcart, 1959; Kerney and Cameron, 1979). The critical structures are the male genitalia, although these often show much intraspecific variation. In most species there is a considerable length of tubular structure (often called epiphallus) between the main swollen part of the penis and the insertion of the retractor muscle. This is not the case in *A. nitidula* and *A. nitens* (Michaud, 1831), in which the retractor appears to insert near the end of the penis. These two species overlap in their distribution, but *A. nitens* occurs further to the south, generally in the mountains. *A. nitens* has a larger, firmer penis. One character often given for their separation is that *A. nitens* has a bipartite penis, but this can be misunderstood because in *A. nitidula* the attachment of the short thick epiphallus to the bulbous part of the penis also suggests a bipartite structure. In *A. nitens* the constriction is nearer the atrium.

The shell of *Aegopinella nitidula* might be confused with other zonitid genera. Four species of *Oxychilus* have been introduced into North America from the Palearctic (Turgeon *et al.*, 1998), and three of these (*O. alliarius, O. cellarius* and *O. draparnaudi*) occur in British Columbia (Forsyth, 1999). These lack the fine spiral lines of *Aegopinella*, appear glossy rather than waxy, and have proportionally smaller umbilici. *O. alliarius* is the *Oxychilus* species most likely to be confused with *A. nitidula*, but the smell of garlic usually produced by the animal when irritated is distinctive. *Zonitoides arboreus* (Say, 1816) and *Z. nitidus* (Müller, 1774) have smaller shells that are more coarsely sculptured and without the paler area around the umbilicus. *Z. arboreus* usually has very fine spiral striae (evident only with at least 50x magnification) but these are much weaker than spiral striae on the shell of *A. nitidula*. The animal of *Z. arboreus* is light grayish or nearly white with darker gray pigment dorsally and on the tentacles. The shell of *Z. nitidus* lacks spiral striae, and the animal is all black. *Nesovitrea* is a Holarctic genus that is sculpturally unlike *Aegopinella*; the axial sculpture consists of more or less regularly and widely spaced grooves.

OCCURRENCE IN NORTH AMERICA

There are two old records of *Aegopinella nitidula* from North America. A report of *A. nitidula* (as *Retinella nitidula*) from gardens in Oakland, California was discussed by Pilsbry (1946) who doubted the identification and suggested that the record was based on misidentified *Oxychilus alliarius* or *O. cellarius*. B. Roth (pers. comm., 1999) has subsequently confirmed that this record was based upon specimens of *O. alliarius*. Pilsbry also doubted the other old record of *A. nitidula*, from the Northwest Territories, Canada, which dates from the checklist of Dall (1905: 39) who cited *"Vitrea nitidula"* from "Fort Resolution (!) Great Slave Lake". As a convention of his checklist, Dall made use of the exclamation mark to indicate that he had personally examined and verified the record, and further wrote that the locality and identification were "indubitable". Our inquiries into the existence of the material upon which Dall based his identification have not been successful, so this record remains unconfirmed and perhaps should remain thought of as probably erroneous.

With the exceptions of Taylor (1908) and Ellis (1969), who repeated these old records, the literature has ignored the old records of *Aegopinella nitidula* on the authority of Pilsbry (La Rocque, 1953; Turgeon *et al.*, 1998). However, the existence of this species in North America can now be firmly established with the discovery of *A. nitidula* in Vancouver, British Columbia.

For the purposes of the American Fisheries Society list of common names of mollusks (Turgeon *et al.*, 1998), "waxy glass-snail" is suggested. This name is already in use in the literature (Pfleger and Chatfield, 1983) and is favored over other published common names that are misleading or less diagnostic.

ACKNOWLEDGMENTS

A. Riedel (Museum and Institute of Zoology, Polish Academy of Science, Warsaw) kindly confirmed the identification; Barry Roth (University of California, Museum of Paleontology, Berkeley) provided information on the Californian record of *"Retinella nitidula"*; and Tammy Forsyth assisted with field work.

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Dentate *Gulella* of Madagascar (Pulmonata: Streptaxidae)

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Abstract: Based on collections made 1992-1996, 71 species and 8 subspecies of native Madagascan dentate *Gulella* Pfeiffer, 1856 (those having barriers or "teeth" in the aperture), can be recognized: *G. ambalaniranae* sp. nov.; *G. ambanikelia* sp. nov.; *G. ambatovakiae* sp. nov.; *G. ambrensis* sp. nov.; *G. ambrensis andavakoerae* subsp. nov.; *G. ambrensis capdambri* subsp. nov.; *G. ambrensis orangea* subsp. nov.; *G. ambrensis rakotomalalai* subsp. nov.; *G. analamerae* sp. nov.; *G. andreana* Fischer-Piette, Blanc and Vukadinovic, 1974; *G. ankaranensis* Fischer-Piette, Blanc, Blanc and Salvat, 1994; *G. antongilae* sp. nov.; *G. beandreana* sp. nov.; *G. bebokae* sp. nov.; *G. bemarahae* sp. nov.; *G. bemoka* sp. nov.; *G. benjamini* Emberton and Pearce, 2000; *G. benjamini saintelucensis* subsp. nov.; *G. bobaombiae* sp. nov.; *G. bouchardi* Fischer-Piette, Blanc and Vukadinovic, 1974; *G. boucheti* Fischer-Piette, Blanc, Blanc and Salvat, 1994; *G. capmini* sp. nov.; *G. celestinae* sp. nov.; *G. columna* sp. nov.; *G. constricta* sp. nov.; *G. fischerpiettei* sp. nov.; *G. fischerpiettei enigma* subsp. nov.; *G. fotobohitrae* sp. nov.; *G. gallorum* Fischer-Piette, Blanc and Salvat, 1975; *G. griffithsi* sp. nov.; *G. hafa* sp. nov.; *G. hafahafa* sp. nov.; *G. jaominai* sp. nov.; *G. josephinae* sp. nov.; *G. kelibea* sp. nov.; *G. lohabea* sp. nov.; *G. lubeti* Fischer-Piette, Blanc, Blanc and Salvat, 1994; *G. magnifica* sp. nov.; *G. magnorchida* sp. nov.; *G. mahafinaratra* sp. nov.; *G. mahagaga* sp. nov.; *G. mahia* sp. nov.; *G. manomboae* sp. nov.; *G. marojejyae* sp. nov.; *G. masoalae* sp. nov.; *G. miaranoniae* sp. nov.; *G. miaryi* Fischer-Piette and Bedoucha, 1964; *G. michellae* sp. nov.; *G. microdon* (Morelet, 1860); *G. microstriata* sp. nov.; *G. mihomehia* sp. nov.; *G. mitsikia* sp. nov.; *G. nakamaroa* sp. nov.; *G. namorokae* sp. nov.; *G. nifikelia* sp. nov.; *G. nosybei* sp. nov.; *G. orchida* sp. nov.; *G. pearcei* sp. nov.; *G. petitboucheti* sp. nov.; *G. pseudandreana* sp. nov.; *G. rakotoarisoni* sp. nov.; *G. ranomasina* sp. nov.; *G. razafyi* sp. nov.; *G. reeae* Emberton and Pearce, 2000; *G. rubinsterni* Fischer-Piette, Blanc, Blanc and Salvat, 1994; *G. rugosa* sp. nov.; *G. satisfacta* Fischer-Piette, Blanc, Blanc and Salvat, 1994; *G. satisfacta charlesblanci* subsp. nov.; *G. satisfacta vitsia* subsp. nov.; *G. soulaiana* Fischer-Piette in Fischer-Piette, Cauquoin and Testud, 1973; *G. tendronia* sp. nov.; *G. tsara* sp. nov.; *G. tsaratananae* sp. nov.; *G. vakinifia* sp. nov.; *G. vatosoa* sp. nov.; *G. vavakelia* sp. nov.; *G. vohimarae* sp. nov.; and *G. zanaharyi* sp. nov. (*G. cerea* [Dunker, 1848], a Comoran species with a single unsubstantiated report from Madagascar, is dropped from the faunal list.)

A dichotomous key is given to these species plus the introduced *Gulella bicolor* (Hutton, 1834). Conchological descriptions are given of all the species. All species are illustrated except *G. bicolor, G. bouchardi, G. lubeti, G. miaryi, G. microdon, G. rubinsterni,* and *G. soulaiana*, for which refer to the *Faune de Madagascar* (Fischer-Piette *et al.*, 1994, vol. 83, pp. 1-551). Edentate *Gulella* of Madagascar (8 species) are treated in a separate paper.

Key Words: Gastropoda, Stylommatophora, land snails, taxonomy, shell variation

This paper is the second in a series on the conchological identification of Madagascar's lesser-known land-snail groups, based on extensive collections made in 1992-1996, and supplemental to the *Faune de Madagascar* monographs of Fischer-Piette *et al.* (1993, 1994). The first paper in the series treated the streptaxid genus *Edentulina* Pfeiffer, 1856 (11 species; Emberton, 1999). The third paper treats the alycaeid endemic genus *Boucardicus* Fischer-Piette and Bedoucha, 1965 (177 species, 6 subspecies; Emberton, in press a); the fourth treats the streptaxid endemic *Parvedentulina* Emberton and Pearce, 2000 (95 species) along with the conchologically similar edentate *Gulella* (8 species; Emberton, in press b); and other papers are in preparation.

Gulella Pfeiffer, 1856 (*sensu* Fischer-Piette *et al.*, 1994, who separate *Gonospira* Swainson, 1840), comprises one of the most diverse radiations within the widespread, carnivorous family Streptaxidae. Native *Gulella* seem to be restricted to Africa and Madagascar and adjacent islands, although some species have been introduced to other tropical regions (Zilch, 1959-1960; Richardson, 1988). The recent pulmonate gastropod volume of the *Faune de Madagascar* (Fischer-Piette *et al.*, 1994) summarized then current knowledge of that island's dentate *Gulella*, listing 13 species.

The author's survey of Madagascar's land molluscs (Emberton, 1994: fig. 1) was completed in 1996 and has resulted in extensive collections of dentate *Gulella* that are reported on here.

LOCALITIES

Of the 1,126 stations collected 1992-1996, the following 261 yielded *Gulella*. Station numbers are in the MBI series. Person-hours refer to actual search time for specimens at the station. Liters of litter refer to the unsieved volume of litter or litter-plus-soil that was collected and later dried, sieved, and sorted.

6. Forêt Ste. Luce, 24°46'30"S, 47°09'00"E, 10 m, coastal rainforest, 29-Jan-95, 6 person-hr.

31. Manombo Reserve, 23°00'50"S, 47°44'00"E, 50 m, rainforest, 20-Apr-95, 27 person-hr.

32. Miaranony, E Ranomafana National Park, 21°10'05"S, 47°33'20"E, 630 m, rainforest, 25-Apr-95, 10 person-hr.

42. E. Morondava, 20°23'35"S, 44°48'05"E, 75 m, dry deciduous forest, 11-May-95, 2 person-hr, 4 l litter.

43. 6.8 W Ankilozato, 20°22'15"S, 45°00'11"E, 205 m, riverine deciduous forest, 11-May-95, 4 person-hr, 3 l litter.

49. 9.6 SSW Mania River bridge, 19°49'59"S, 45°31'12"E, 65 m, gully forest of palmetto and scrub, 12-May-95, 3 person-hr, 2 l litter.

52. 0.2km E Antanandava, 16°07'40"S, 45°28'40"E, 40 m, scrub forest, 18-May-95.

55-74. Namoroka Reserve. 55. 16°23'00"S, 45°21'30"E, 110 m, dry deciduous forest, 21-May-95, 185 person-hr, 4 l litter. 56. 16°21'48"S, 45°19'04"E, 100 m, dry deciduous-baobab forest, 22-May-95, 176 person-hr, 2 l litter. 58. 16°25'18"S, 45°23'27"E, 120 m, dry deciduous forest, 23-May-95, 28 person-hr. 61. 16°23'20"S, 45°18'25"E, 105 m, dry deciduous forest, 25-May-95, 176 person-hr, 1 l litter. 62. 16°24'00"S, 45°17'58"E, 90 m, hardwood forest, 26-May-95, 144 person-hr. 63. 16°23'07"S, 45°18'41"E, 75 m, dry deciduous forest, 27-May-95, 3 l litter. 64. 16°23'26"S, 45°18'10"E, 90 m, raffia swamp, 27-May-95, 42 person-hr, 2 l litter. 65. 16°23'26"S, 45°18'10"E, 90 m, raffia swamp, 27-May-95, 45 person-hr. 67. 16°23'15"S, 45°20'45"E, 110 m, dry deciduous forest, 24-May-95, 47 person-hr, 1 l litter. 68. 16°22'50"S, 45°20'50"E, 85 m, dry deciduous forest, 24-May-95, 45 person-hr, 1 l litter. 69. 16°22'35"S, 45°19'30"E, 95 m, dry deciduous forest, 25-May-95, 76 person-hr, 1 l litter. 70. 16°22'35"S, 45°20'05"E, 115 m, dry deciduous forest, 25-May-95, 60 person-hr, 1 l litter. 71. 16°23'45"S, 45°21'30"E, 100 m, dry deciduous forest, 26-May-95, 72 person-hr, 1 l litter. 72. 16°23'30"S, 45°21'15"E, 125 m, dry deciduous forest, 26-May-95, 34 person-hr, 1 l litter. 73. 16°24'50"S, 45°20'55"E, 115 m, dry deciduous forest, 27-May-95, 10 person-hr, 1 l litter. 74. 16°23'00"S, 45°20'20"E, 100 m, dry deciduous forest, 28-May-95, 14 person-hr, 2 l litter.

81-84. Ampijoroa Reserve, 16°17'28"S, 46°49'13"E, 20 m, dry deciduous forest, 2-Jun-95, 4 person-hr, 2 l litter. 82. 16°17'18"S, 46°49'16"E, 20 m, dry deciduous forest, 2-Jun-95, 14 person-hr, 2 l litter. 83. 16°17'19"S, 46°49'35"E, 95 m, hardwood deciduous forest, 3-Jun-95, 102 person-hr, 3 l litter. 84. 16°17'01"S, 46°49'12"E, 85 m, dry deciduous forest, 4-Jun-95, 2 person-hr, 2 l litter.

95-115. Tsaratanana Reserve. 95. 14°02'35"S, 48°46'28"E, 1160 m, rainforest, 13-Jun-95, 7 person-hr, 1 l litter. 98. 14°02'52"S, 48°47'09"E, 950 m, rainforest, 14-Jun-95, 28 person-hr. 103. 14°02'12"S, 48°46'20"E, 865 m, rainforest, 16-Jun-95, 10 person-hr. 105. 14°02'12"S, 48°46'15"E, 770 m, rainforest, 16-Jun-95, 7 person-hr. 106. 14°02'12"S, 48°46'15"E, 740 m, rainforest, 17-Jun-95, 10 person-hr. 107. 14°02'00"S, 48°46'07"E, 685 m, rainforest, 17-Jun-95. 108. 14°01'50"S, 48°46'00"E, 630 m, rainforest, 17-Jun-95, 16 person-hr. 110. 14°01'40"S, 48°45'50"E, 540 m, rainforest, 18-Jun-95, 10 person-hr. 111. 14°01'40"S, 48°45'45"E, 500 m, rainforest, 18-Jun-95, 10 person-hr. 112. 14°01'40"S, 48°45'40"E, 480 m, rainforest, 18-Jun-95, 12 person-hr. 114. 14°01'40"S, 48°45'35"E, 445 m, rainforest, 19-Jun-95, 5 person-hr. 115. 14°01'35"S, 48°45'35"E, 420 m, rainforest, 19-Jun-95, 1 person-hr.

118. Lokobe Reserve, 13°25'00"S, 48°18'40"E, 60 m, rainforest, 25-Jun-95, 15 person-hr, 3 l litter.

168. Galoko Escarpment, 13°34'30"S, 48°45'16"E, 225 m, hardwood-palm-pandanus forest, 4-Jul-95, 14 person-hr, 2 l litter.

170-195. Montagne d'Ambre National Park. 170. 12°32'55"S, 49°09'50"E, 1250 m, 8-Jul-95, 5 person-hr. 172. 12°35'46"S, 49°09'35"E, 1325 m, montane rainforest, 8-Jul-95, 15 person-hr, 2 l litter. 178. 12°37'09"S, 49°10'26"E, 1135 m, montane rainforest, 9-Jul-95, 6 person-hr, 2 l litter. 181. 12°37'22"S, 49°10'28"E, 1040 m, rainforest, 9-Jul-95, 17 person-hr, 2 l litter. 182. 12°37'25"S, 49°10'30"E, 1095 m, montane rainforest, 10-Jul-95, 5 person-hr, 2 l litter. 184. 12°36'46"S, 49°09'57"E, 1165 m, rainforest, 10-Jul-95, 14 person-hr, 2 l litter. 185. 12°36'35"S, 49°09'52"E, 1205 m, rainforest, 10-Jul-95, 6 person-hr, 2 l litter. 192. 12°35'04"S, 49°08'46"E, 1235 m, rainforest, 12-Jul-95, 6 person-hr, 2 l litter. 193. 12°34'34"S, 49°09'25"E, 1305 m, rainforest, 12-Jul-95, 6 person-hr, 2 l litter. 195. 12°31'42"S, 49°10'16"E, 1050 m, rainforest, 12-Jul-95, 9 person-hr, 2 l litter.

199-214. Analamera Reserve. 199. 12°43'46"S, 49°28'50"E, 35 m, dry deciduous forest, 15-Jul-95, 7 person-hr, 2 l litter. 201. 12°44'28"S, 49°30'21"E, 315 m, dry deciduous forest, 15-Jul-95, 30 person-hr, 2 l litter. 202. 12°44'32"S, 49°30'20"E, 310 m, dry deciduous forest, 16-Jul-95. 203. 12°44'35"S, 49°30'16"E, 285 m, bamboo-dry deciduous thicket, 16-Jul-95, 11 person-hr, 2 l litter. 204. 12°44'38"S, 49°30'13"E, 235 m, dry deciduous forest, 16-Jul-95, 11 person-hr, 2 l litter. 206. 12°44'42"S, 49°30'08"E, 195 m, dry deciduous forest, 16-Jul-95, 11 person-hr, 2 l litter. 207. 12°44'43"S, 49°30'06"E, 150 m, dry deciduous forest, 16-Jul-95. 208. 12°44'45"S, 49°30'04"E, 100 m, dry deciduous forest, 16-Jul-95, 6 person-hr, 2 l litter. 210. 12°44'49"S, 49°29'57"E, 35 m, dry deciduous floodplain forest, 16-Jul-95, 8 person-hr, 2 l litter. 212. 12°43'46"S, 49°28'53"E, 35 m, 16-Jul-95. 213. 12°44'50"S, 49°29'40"E, 30 m, dry deciduous floodplain forest, 16-Jul-95, 30 person-hr, 2 l litter. 214. 12°42'09"S, 49°27'61"E, 20 m, dry deciduous forest, 16-Jul-95, 5 person-hr, 2 l litter.

215-218. Montagne des Orchides. 215. 12°23'31"S, 49°19'41"E, 295 m, dry deciduous forest, 20-Jul-95, 14 person-hr, 2 l litter. 217. 12°23'23"S, 49°19'45"E, 360 m, dry deciduous forest, 20-Jul-95, 18 person-hr, 2 l litter. 218. 12°23'25"S, 49°19'48"E, 385 m, dry deciduous forest, 20-Jul-95, 16 person-hr, 2 l litter.

221. Montagne des Français. 221. 12°19'30"S, 49°20'22"E, 300 m, secondary dry deciduous forest, 21-Jul-95, 12 person-hr, 3 l litter. 222. 12°19'20"S, 49°20'20"E, 230 m, dry deciduous forest, 21-Jul-95, 5 person-hr, 2 l litter. 223. 12°18'55"S, 49°20'15"E, 70 m, dry deciduous forest, 21-Jul-95, 3 person-hr, 1 l litter.

224-225. Baie des Dunes, Cap Mine, edge of Forêt d'Orange. 224. 12°14'40"S, 49°22'43"E, 03 m, scrub, 21-Jul-95, 4 person-hr, 2 l litter. 225. Baie des Dunes, 12°14'20"S, 49°22'25"E, 06 m, scrub, 21-Jul-95, 1 person-hr, 2 l litter.

229-241. N Cap d'Ambre. 229. near lighthouse, 11°57'30"S, 49°16'35"E, 05 m, euphorb scrub forest, 24-Jul-95, 9 person-hr, 2 l litter. 230. near lighthouse, 11°57'48"S, 49°16'33"E, 20 m, dry deciduous forest, 24-Jul-95, 5 person-hr, 2 l litter. 233. near lighthouse, 11°58'00"S, 49°16'40"E, 10 m, deciduous-baobab forest, 24-Jul-95, 11 person-hr, 2 l litter. 234. near Bemoka, 11°59'00"S, 49°16'30"E, 25 m, dry deciduous forest, 24-Jul-95, 6 person-hr, 2 l litter. 238. near Ambatojanahary, 12°00'14"S, 49°17'52"E, 40 m, baobab-deciduous forest, 25-Jul-95, 49 person-hr, 2 l litter. 239. near Ambatojanahary, 12°00'10"S, 49°17'50"E, 40 m, dry deciduous forest, 25-Jul-95, 22 person-hr, 2 l litter. 240. near Ambatojanahary, 12°00'00"S, 49°17'50"E, 05 m, dry deciduous forest, 25-Jul-95, 12 person-hr, 2 l litter. 241. near Ambatojanahary, 12°00'03"S, 49°17'27"E, 15 m, dry deciduous forest, 25-Jul-95, 6 person-hr, 2 l litter.

245-255. S Bemaraha Reserve. 245. 19°08'36"S, 44°48'54"E, 70 m, dry forest, 14-Jun-95, 9 person-hr, 6 l litter. 247. 19°08'06"S, 44°52'54"E, 100 m, lush tall riverine gallery forest, 15-Jun-95, 9 person-hr. 248. 19°07'36"S, 44°52'54"E, 100 m, lush tall riverine gallery forest, 15-Jun-95, 4 person-hr. 249. 19°08'06"S, 44°50'36"E, 100 m, tall riverine gallery forest, 16-Jun-95, 4 person-hr. 250. 19°08'12"S, 44°49'42"E, 80 m, tall riverine gallery forest, 16-Jun-95, 3 person-hr. 251. 19°07'36"S, 44°48'36"E, 70 m, dry forest, 17-Jun-95, 8 person-hr. 252. 19°07'48"S, 44°48'54"E, 70 m, dry, flood prone forest, 17-Jun-95, 2 person-hr. 254. 19°02'24"S, 44°48'00"E, 150 m, forest along limestone wall, 18-Jun-95, 6 person-hr. 255. 19°00'48"S, 44°46'54"E, 150 m, tall forest in limestone slots, 19-Jun-95, 9 person-hr.

256-257. S of Vohimar, 13°35'05"S, 49°59'32"E, viny rainforest, 2-Sep-95. 256. 90 m, 8 person-hr, 2 l litter. 257. 70 m, 1 person-hr.

258-267. Ambalanirana Mountain. 258. 13°50'56"S, 49°59'27"E, 210 m, rainforest, 3-Sep-95, 27 person-hr, 2 l litter. 259. 13°50'S, 49°59'E, 350 m, rainforest, 3-Sep-95. 260. 13°50'S, 49°59'E, 561 m, rainforest, 3-Sep-95, 31 person-hr, 2 l litter. 261. 13°50'S, 49°59'E, 500 m, rainforest, 4-Sep-95, 47 person-hr, 2 l litter. 262. 13°50'S, 49°59'E, 400 m, viny rainforest, 4-Sep-95, 56 person-hr, 2 l litter. 263. 13°50'S, 49°59'E, 400 m, rainforest, 4-Sep-95. 264. 13°50'S, 49°59'E, 300 m, palm rainforest, 4-Sep-95, 68 person-hr, 2 l litter. 265. 13°50'44"S, 49°59'48"E, 465 m, palm rainforest, 5-Sep-95, 38 person-hr, 2 l litter. 266. 13°50'S, 49°59'E, 400 m, rainforest, 5-Sep-95, 38 person-hr, 2 l litter. 267. 13°50'S, 49°59'E, 315 m, rainforest, 5-Sep-95, 68 person-hr, 2 l litter.

270. Andranomena Forest, N of Sambava, 13°56'29"S, 50°05'02"E, 20 m, rainforest, 8-Sep-95, 22 person-hr, 2 l litter.

279-314. W Masoala Peninsula. 279. 15°54'50"S, 50°04'20"E, 60 m, hardwood-pandanus rainforest, 15-Sep-95, 18 person-hr. 282. 15°52'55"S, 50°01'11"E, 50 m, hardwood rainforest, 15-Sep-95, 10 person-hr. 283. 15°52'45"S, 50°01'55"E, 60 m, hardwood rainforest, 16-Sep-95, 17 person-hr, 2 l litter. 284. 15°52'20"S, 50°02'15"E, 05 m, hardwood-pandanus rainforest, 16-Sep-95, 9 person-hr. 285. 15°52'15"S, 50°02'15"E, 20 m, hardwood rainforest, 16-Sep-95, 9 person-hr. 289. 15°51'00"S, 50°02'00"E, 180 m, hardwood-pandanus-palm rainforest, 16-Sep-95, 9 person-hr. 294. 15°48'25"S, 50°03'05"E, 130 m, hardwood-palm forest, 18-Sep-95, 38 person-hr, 2 l litter. 295. 15°48'05"S, 50°03'10"E, 310 m, hardwood-pandanus forest, 18-Sep-95, 42 person-hr, 2 l litter. 300. 15°47'20"S, 50°03'50"E, 350 m, hardwood rainforest, 20-Sep-95, 39 person-hr, 2 l litter. 303. 15°48'22"S, 50°03'00"E, 220 m, hardwood-palm rainforest, 22-Sep-95, 44 person-hr, 2 l litter. 306. 15°33'S, 50°00'E, 430 m, 25-Sep-95. 307. 15°33'45"S, 50°00'15"E, 680 m, hardwood rainforest, 25-Sep-95, 66 person-hr, 2 l litter. 310. 15°33'45"S, 50°00'25"E, 840 m, hardwood-pandanus forest, 26-Sep-95, 45 person-hr, 2 l litter. 311. 15°33'30"S, 49°59'50"E, 430 m, hardwood rainforest, 27-Sep-95, 45 person-hr. 313. 15°33'27"S, 49°59'40"E, 305 m, hardwood rainforest, 28-Sep-95, 45 person-hr, 2 l litter. 314. 15°33'25"S, 49°59'25"E, 180 m, hardwood rainforest, 28-Sep-95, 45 person-hr, 2 l litter.

342. Mt. Mahalevona, E of Maroantsetra, 15°25'12"S, 49°57'05"E, 925 m, hardwood-palm rainforest, 11-Oct-95, 28 person-hr, 2 l litter.

349-358. W of Sahasoa, S of Mananara. 349. 16°19'20"S, 49°44'55"E, 480 m, hardwood rainforest, 18-Oct-95, 57 person-hr, 4 l litter. 351. 16°19'35"S, 49°44'30"E, 515 m, hardwood-pandanus forest, 18-Oct-95, 36 person-hr, 2 l litter. 353. 16°19'35"S, 49°44'00"E, 465 m, hardwood rainforest, 19-Oct-95, 47 person-hr, 2 l litter. 354. 16°19'35"S, 49°44'25"E, 515 m, hardwood-pandanus forest, 19-Oct-95, 14 person-hr. 355. 16°19'35"S, 49°44'29"E, 510 m, hardwood-pandanus forest, 19-Oct-95, 17 person-hr. 356. 16°19'37"S, 49°45'57"E, 350 m, hardwood-pandanus forest, 20-Oct-95, 36 person-hr. 357. 16°19'20"S, 49°46'50"E, 330 m, hardwood rainforest, 21-Oct-95, 30 person-hr. 358. 16°19'30"S, 49°47'45"E, 330 m, hardwood-ravenala forest, 21-Oct-95, 27 person-hr, 2 l litter.

363-364. NW of Manompona, S of Mananara 363. 16°39'50"S, 49°40'40"E, 240 m, hardwood rainforest, 24-Oct-95, 30 person-hr, 1 l litter. 364. 16°39'48"S, 49°41'25"E, 160 m, hardwood rainforest, 25-Oct-95, 3 person-hr.

366-367. Isle Ste. Marie. 366. 16°55'07"S, 49°53'15"E, 110 m, hardwood-palm-ravenala forest, 26-Oct-95, 14 person-hr, 2 l litter. 367. 16°54'45"S, 49°53'05"E, 80 m, hardwood-palm-ravenala forest, 27-Oct-95, 14 person-hr.

400-401. S Cap d'Ambre, la Butte Bobaomby. 400. 12°10'55"S, 49°13'00"E, 70 m, dry deciduous forest, 24-Aug-95, 8 person-hr, 2 l litter. 401. 12°11'45"S, 49°13'00"E, 205 m, dry deciduous-baobab forest, 24-Aug-95, 32 person-hr, 2 l litter.

403-407. S Cap d'Ambre, Ambongoabo. 403. 12°15'55"S, 49°15'20"E, 352 m, scrub, 25-Aug-95, 4 person-hr, 1 l litter. 404. 12°15'55"S, 49°15'20"E, 340 m, dry deciduous forest, 25-Aug-95, 6 person-hr, 2 l litter. 405. 12°15'55"S, 49°15'27"E, 320 m, baobab-deciduous forest, 25-Aug-95, 12 person-hr. 407. 12°15'55"S, 49°15'40"E, 290 m, dry deciduous forest, 26-Aug-95, 5 person-hr, 2 l litter.

408-411. W of Sakaramy, S of Diego Suarez. 408. 12°26'35"S, 49°13'15"E, 410 m, dry deciduous forest, 26-Aug-95, 20 person-hr, 2 l litter. 411. 12v26'35"S, 49°12'45"E, 380 m, dry deciduous forest, 26-Aug-95, 12 person-hr, 2 l litter.

413-421. Andavakoera, N of Betsiaka. 413. 13°07'44"S, 49°14'05"E, 240 m, dry deciduous forest, 30-Aug-95, 26 person-hr, 2 l litter. 417. 13°06'36"S, 49°13'23"E, 230 m, dry deciduous forest, 30-Aug-95, 62 person-hr, 2 l litter. 418. 13°06'24"S, 49°13'19"E, 115 m, dry deciduous forest, 31-Aug-95, 115 person-hr, 2 l litter. 421. 13°07'S, 49°13'E, 410 m, dry deciduous forest, 1-Sep-95, 26 person-hr, 2 l litter.

423-435. Manombo Reserve, 23°00'50"S, 47°44'00"E, 50 m, rainforest. 423. 21-Apr-95, 528 person-hr. 424. 22-May-95, 256 person-hr. 425. 30-Jun-95, 256 person-hr. 426. 23-Jul-95, 256 person-hr. 427. 23-Aug-95, 256 person-hr. 428. 22-Sep-95, 256 person-hr. 429. 22-Oct-95, 256 person-hr. 430. 22-Nov-95, 256 person-hr, 40 l litter. 431. 22-Dec-95, 256 person-hr. 432. 23-Jan-96, 256 person-hr. 433. 27-Feb-96, 256 person-hr. 434. 23-Mar-96, 256 person-hr. 435. 22-Apr-96, 256 person-hr, 40 l litter.

439-451. Miaranony, E Ranomafana National Park, 21°10'05"S, 47°33'20"E, 630 m, rainforest. 439. 26-Apr-95, 520 person-hr. 440. 27-May-95, 256 person-hr. 441. 5-Jul-95, 256 person-hr. 442. 29-Jul-95, 256 person-hr. 443. 29-Aug-95, 248 person-hr. 444. 28-Sep-95, 248 person-hr. 445. 29-Oct-95, 248 person-hr. 446. 28-Nov-95, 248 person-hr, 40 l litter. 447. 29-Dec-95, 256 person-hr. 448. 28-Jan-96, 248 person-hr. 449. 2-Mar-96, 240 person-hr. 450. 29-Mar-96, 256 person-hr. 451. 28-Apr-96, 256 person-hr, 40 l litter.

458-466. Ambatolahy, next to Ranomafana National Park, 21°13'50"S, 47°25'20"E, 850 m, rainforest. 458. 9-Sep-95, 248 person-hr. 459. 9-Oct-95, 248 person-hr. 460. 9-Nov-95, 248 person-hr, 40 l litter. 461. 14-Dec-95, 248 person-hr. 462. 9-Jan-96, 248 person-hr. 463. 9-Feb-96, 248 person-hr. 464. 9-Mar-96, 248 person-hr. 465. 10-Apr-96, 248 person-hr. 466. 9-May-96, 248 person-hr, 40 l litter.

483-494. N Bemaraha Reserve. 483. 18°01'48"S, 44°31'42"E, 270 m, dry deciduous forest, 22-Jun-96. 484. 18°03'30"S, 44°31'42"E, 250 m, dry deciduous forest, 23-Jun-96. 489. 18°41'36"S, 44°43'06"E, 150 m, semideciduous forest, 27-Jun-96. 490. 18°45'24"S, 44°45'24"E, 280 m, semideciduous forest, 27-Jun-96. 494. 18°45'54"S, 44°45'24"E, 280 m, semideciduous forest, 29-Jun-96.

502-540. Tsaratanana Reserve. 502. 14°01'30"S, 48°45'08"E, 310 m, rainforest, 12-Jun-95, 4 person-hr, 1 l litter. 503. 14°00'58"S, 48°46'10"E, 600 m, rainforest, 12-Jun-95, 5 person-hr, 1 l litter. 504. 14°00'42"S, 48°46'30"E, 730 m, rainforest, 13-Jun-95, 10.5 person-hr, 0.5 l litter. 505. 14°00'24"S, 48°46'30"E, 910 m, rainforest, 13-Jun-95, 10.5 person-hr, 0.5 l litter. 513. 13°59'45"S, 48°47'25"E, 1525 m, rainforest, 14-Jun-95, 7 person-hr, 1 l litter. 514. 13°59'40"S, 48°47'10"E, 1660 m, cloudforest, 14-Jun-95, 4 person-hr, 1 l litter. 527. 13°59'05"S, 48°47'40"E, 1395 m, rainforest, 17-Jun-95, 13 person-hr, 1 l litter. 535. 13°59'20"S, 48°46'32"E, 930 m, rainforest, 18-Jun-95, 6 person-hr, 0.5 l litter. 537. 14°00'06"S, 48°46'30"E, 810 m, savannah, 19-Jun-95, 2 person-hr, 1 l litter. 538. 14°00'04"S, 48°46'35"E, 790 m, rainforest, 19-Jun-95, 7 person-hr, 1 l litter. 540. 14°00'58"S, 48°46'25"E, 700 m, rainforest, 19-Jun-95, 2 person-hr, 1 l litter.

546. Nosy Komba, 13°26'25"S, 48°20'30"E, 10 m, scrub, 23-Jun-95, 2 person-hr.

554-581. Ankarana Reserve. 554. 12°55’35”S, 49°06’55”E, 70 m, dry deciduous forest, 21-Aug-95, 15 person-hr, 2 l litter. 558. 12°54’33”S, 49°06’37”E, 80 m, dry deciduous forest, 22-Aug-95, 14 person-hr, 2 l litter. 561. 12°55’35”S, 49°05’39”E, 30 m, dry deciduous forest, 22-Aug-95, 12 person-hr, 2 l litter. 564. 12°55’26”S, 49°05’12”E, 95 m, dry deciduous forest, 22-Aug-95, 19 person-hr, 2 l litter. 565. 12°55’33”S, 49°05’28”E, 40 m, dry deciduous forest, 22-Aug-95, 10 person-hr, 2 l litter. 566. 12°56’09”S, 49°07’13”E, 90 m, dry deciduous forest, 23-Aug-95, 14 person-hr, 2 l litter. 568. 12°56’43”S, 49°07’29”E, 125 m, dry deciduous forest, 23-Aug-95, 6 person-hr, 4 l litter. 570. 12°57’22”S, 49°07’05”E, 45 m, dry deciduous forest, 24-Aug-95, 6 person-hr, 2 l litter. 571. 12°57’24”S, 49°07’05”E, 85 m, dry deciduous forest, 24-Aug-95, 9 person-hr, 2 l litter. 572. 12°57’26”S, 49°07’05”E, 110 m, dry deciduous forest, 24-Aug-95, 5 person-hr, 2 l litter. 576. 12°58’26”S, 49°06’54”E, 90 m, dry deciduous forest, 25-Aug-95, 10 person-hr, 2 l litter. 577. 12°58’39”S, 49°06’30”E, 100 m, dry deciduous forest, 25-Aug-95, 13 person-hr, 2 l litter. 579. 12°58’53”S, 49°06’03”E, 100 m, dry deciduous forest, 25-Aug-95, 14 person-hr, 2 l litter. 580. 12°58’56”S, 49°05’49”E, 95 m, dry deciduous forest, 26-Aug-95, 21 person-hr, 4 l litter. 581. 12°58’50”S, 49°06’35”E, 110 m, dry deciduous forest, 26-Aug-95, 6.5 person-hr, 2 l litter.

593-612. Marojejy Reserve. 553. 14°26’12”S, 49°44’36”E, 1300 m, rainforest, 14-Sep-95, 12 person-hr, 2 l litter. 612. 14°26’05”S, 49°46’20”E, 520 m, rainforest, 18-Sep-95, 16 person-hr, 2 l litter.

627-649. W Marojejy Reserve. 627. 14°28’00”S, 49°35’30”E, 900 m, rainforest, 25-Sep-95, 7 person-hr, 2 l litter. 634. 14°28’10”S, 49°35’30”E, 1170 m, rainforest, 25-Sep-95, 14 person-hr, 2 l litter. 645. 14°28’53”S, 49°33’40”E, 960 m, rainforest, 27-Sep-95, 6 person-hr, 2 l litter. 648. 14°29’20”S, 49°33’35”E, 805 m, rainforest, 28-Sep-95, 23 person-hr, 2 l litter. 649. 14°29’40”S, 49°34’00”E, 700 m, rainforest, 28-Sep-95, 24 person-hr, 2 l litter.

650-677. E of Marojejy Reserve. 650. 14°S, 49°E, 200 m, moist forest, 29-Sep-95. 661. 14°32’38”S, 49°42’15”E, 1100 m, rainforest, 4-Oct-95, 6 person-hr, 2 l litter. 666. 14°32’38”S, 49°42’05”E, 1400 m, cloudforest with bamboo, 5-Oct-95, 8 person-hr, 4 l litter. 668. 14°32’39”S, 49°42’00”E, 1500 m, cloudforest with bamboo, 5-Oct-95, 5 person-hr, 4 l litter. 671. 14°32’37”S, 49°42’14”E, 1300 m, rainforest, 5-Oct-95, 7 person-hr, 4 l litter. 674. 14°32’30”S, 49°42’10”E, 880 m, rainforest, 6-Oct-95, 10 person-hr, 4 l litter. 677. 14°31’35”S, 49°43’55”E, 315 m, rainforest, 7-Oct-95, 10 person-hr, 4 l litter.

679. 2km N Mandena, ca 14°28’S, ca 49°55’E, 15-Oct-95, 40 person-hr.

680. 5km NE Manantenina, 14°27’S, 49°49’E, 16-Oct-95, 40 person-hr.

711-714. near Ampanifena, near Mt. Ambalanirana, 13°51’S, 49°59’E, 25-Oct-95. 711. 300 m, 192 person-hr. 712. 350 m, 840 person-hr. 714. 300 m, 32 person-hr.

715-717. near Mandena, ca 14°28’S ca 49°55’E, 25-Oct-95. 715. 25-Oct-95, 16 person-hr, 5 l litter. 716. 16 person-hr, 2 l litter. 717. 16 person-hr, 4 l litter.

723-724. Soanierana Ivongo. 723. 16°55’30”S, 49°35’12”E, 20 m, introduced eucalyptus forest, 11-Nov-95, 3 person-hr, 3 l litter. 724. 16°55’32”S, 49°35’12”E, 60 m, degraded scrub, 11-Nov-95, 2 person-hr, 2 l litter.

742-766. Ambatovaky Reserve. 742. 16°47’17”S, 49°08’11”E, 890 m, rainforest with pandanus, 20-Nov-95, 16 person-hr, 4 l litter. 744. 16°46’58”S, 49°08’21”E, 1025 m, rainforest with pandanus, 21-Nov-95, 10 person-hr, 8 l litter. 756. 16°44’47”S, 49°10’38”E, 675 m, rainforest with pandanus, 22-Nov-95, 5 person-hr, 2 l litter. 758. 16°42’50”S, 49°10’27”E, 605 m, rainforest, 23-Nov-95, 7 person-hr, 2 l litter. 766. 16°43’26”S, 49°23’10”E, 400 m, rainforest, 27-Nov-95, 6 person-hr, 2 l litter.

802-816. Ankarana Reserve. 802. 13°00’18”S, 49°00’18”E, 50 m, 8-Oct-94. 803. 13°00’00”S, 49°01’00”E, 50 m, 8-Oct-94. 805. 13°01’24”S, 49°00’00”E, 50 m, 8-Oct-94. 807. 12°54’24”S, 49°06’42”E, 90 m, 10-Oct-94. 810. 12°54’54”S, 49°06’18”E, 90 m, 10-Oct-94. 813. 12°57’54”S, 49°08’18”E, 150 m, 11-Oct-94. 814. 12°56’48”S, 49°07’42”E, 70 m, 11-Oct-94. 815. 12°55’42”S, 49°03’18”E, 100 m, 12-Oct-94. 816. 12°55’48”S, 49o03’18”E, 100 m, 12-Oct-94.

818. Betsiboka River, 16°57’S, 46°57’E, 135 m, 14-Oct-94.

1342. 23.9 km S of Farafangana, 23°00’00”S, 47°44’30”E, 60 m, 14-Sep-92, 28 person-hr.

1347-1351. Manombo Reserve. 1347. 23°01’40”S, 47°44’00”E, 50 m, 15-Sep-92. 1351. 23°01’00”S, 47°44’00”E, 50 m, native forest, 16-Sep-92, 480 person-hr.

1389-1391. Fotobohitra, 21°21’40”S, 47°51’20”E, 27-Sep-92. 1389. 350 m, rainforest, 16 person-hr. 1391. 320 m, ravenala forest, 6 person-hr.

1402. near Andringitra Reserve, 22°04’S, 46°54’E, 1400 m, primary forest, 3-Oct-92, 36 person-hr.

1419. Pic Saint Louis, near Ft. Dauphin, 25°00’30”S, 46°57’45”E, rainforest, 530 m, 10-Oct-92, 5 person-hr.

1529-1549. Betampona Reserve, rainforest. 1529. 17°54’15”S, 49°12’40”E, 600 m, 13-May-93, 1.7 person-hr. 1536. 17°54’00”S, 49°12’35”E, 540 m, 14-May-93, 9 person-hr. 1540. 17°54’25”S, 49°13’25”E, 530 m, 15-May-93, 4 person-hr. 1545. 17°55’15”S, 49°13’15”E, 560 m, 16-May-93, 4 person-hr. 1547. 17°55’35”S, 49°13’10”E, 400 m, 16-May-93, 6 person-hr. 1549. 17°54’S, 49°12’E, 400 m, 16-May-93.

METHODS AND MATERIALS

Materials were collected 1992-1996, using methods advocated in Emberton *et al.* (1996).

Table 1 and Fig. 1 show the characters used. Because of Madagascar’s continuing environmental crisis and the urgency it puts upon providing taxonomic data to conservationists and systematists, I have examined only shell morphology and have generally assessed characters visible only in apertural and apical views. Despite these restrictions, the resulting 30 characters (Fig. 1, Table 1) seemed adequate, with key additions in a few special cases (Tables 2 and 4), for an initial pass at delimiting taxa within this complex and rather difficult group.

I have attempted to apply Templeton’s (1989) cohesion concept of species. Disjunct shell morphologies occurring in sympatry with no intermediates I considered distinct species (there is no sexual dimorphism, as *Gulella* are hermaphroditic). I then used the degrees of conchological differences between such sympatric species as guidelines for delimiting allopatric species, also comparing ecologies and searching for additional shell characters to resolve borderline cases.

Within especially variable species, I selected not only a standard representative but also one to three extreme variants for description and/or illustration. Geographically separated, morphologically discrete, extreme variants I deemed subspecies only if they seemed well isolated by discontinuous habitat. I photographed shells at standard

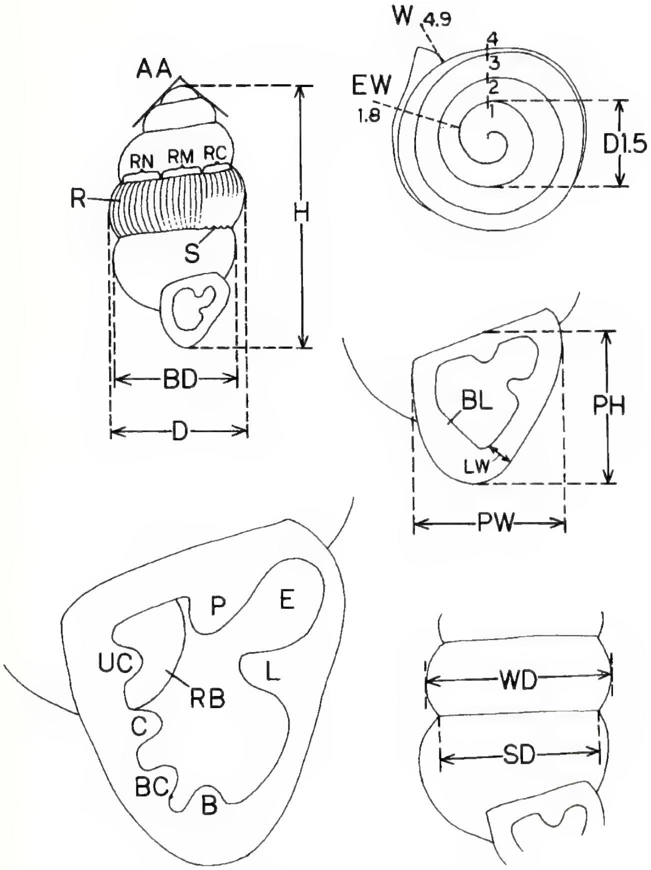

Fig. 1. Characters (see Table 1). Abbreviations: AA, apical angle; B, baso-central tooth; BC, baso-columellar tooth; BD, body-whorl diameter; BL, baso-columellar lamella; C, mid-columellar tooth; D, mid-shell greatest diameter; D1.5, diameter of first 1.5 whorls; E, parieto-palatal embayment; EW, embryonic whorl count; H, shell height; L, palatal tooth; LW, apertural lip width; P, parietal tooth; PH, peristome height; PW, peristome width, R, rib sculpture, RB, columellar recessed baffle; RC, complete diminution of rib sculpture; RM, moderate diminution of rib sculpture; RN, no diminution of rib sculpture; S, sutural crenulation; SD, sutural diameter; UC, upper-columellar tooth; W, whorl count; WD, whorl diameter used in calculating sutural depth.

magnifications (6.4x, 10x, 16x, 25x, and 40x) in apertural view. For identifications and diagnoses, I referred to Fischer-Piette *et al.* (1994) and Emberton and Pearce (2000) for Madagascar; Griffiths (1996, and his unpublished, illustrated catalog) for the Mascarenes; Hanley and Theobald (1876) and Blanford and Godwin-Austen (1908) for India and Sri Lanka; and Moellendorff and Kobelt (1905), Pilsbry (1919), Germain (1923), Connolly (1939), Verdcourt (1961-1993), Bruggen (1965-1980), and Winter (1996) for Africa, Aldabra, and the Comoros.

RESULTS

Table 2 compares the 14 most similar sympatric-species pairs I detected. The 7 pairs diagnosable by apertur-

Table 1. Characters used (see Fig. 1). Measurements were taken by ocular micrometer on a dissecting microscope or by millimeter rule on a photograph. For maximum accuracy, all ratios were calculated using unconverted measurement units. Some additional shell characters used in distinguishing cryptic species and subspecies are given in Tables 2 and 4.

Shell Size and Shape

1) Height (H), to 0.1 mm
2) Diameter (D), mid-shell greatest, to 0.1 mm
3) Height/diameter = H/D, to 0.1
4) Whorl count (W), starting at the engraved, straightish line marking the beginning of the suture, as seen at 40x magnification under narrow-beam, perpendicular side lighting, to 0.1 whorl (0.05 whorl for Table 3)
5) Coiling-tightness index = W/lnH, where W = whorl count, H = shell height, and ln = natural logarithm (base e)
6) Apical angle (AA), to 5°
7) Barreling index (percent barreling) = 100((D-BD)/D), where D = greatest mid-shell diameter, and BD = the body-whorl diameter above and not including the peristome

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Suture and Sculpture of Penultimate and Body Whorls

8) Sutural depth index = 100((WD-SD)/WD), where SD = diameter along a major suture, and WD = parallel greatest diameter of the whorl just above that suture
9) Sutural crenulation (S): none, weak, moderate, or strong
10) Rib-sculpture (R) strength near upper suture: none, weak, moderate, or strong
11) Rib-sculpture diminishment from upper suture to lower suture: none (RN), moderate (RM), or complete (RC)

Embryonic Shell Size and Sculpture

12) Embryonic whorl count (EW), to 0.1 whorl
13) Diameter of first 1.5 whorls (D1.5), measured at 40x magnification, to 0.01 mm (0.001 mm for Table 3)
14) Embryonic sculpture as seen at 40x magnification under narrow-beam side lighting: description

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Apertural Size and Shape

15) Peristome height (PH), to 0.1 mm
16) Peristome width (PW), to 0.1 mm
17) Peristome height/width, to 0.1
18) Peristome width/shell diameter, to 0.1
19) Apertural lip width (LW), to 0.01 mm
20) Apertural lip width/peristome width, to 0.01

Apertural Barriers

21) Parietal tooth (P) size (minute, small, moderate, large, or massive) and whether notched or bifid
22) Palatal tooth (L) presence/absence, size (minute, small, moderate, large, or massive), and shape (description)
23) Parieto-palatal embayment (E) size: narrow, moderately wide, or wide
24) Columellar recessed baffle (RB) (= submerged columellar fold or lobe of Pilsbry, 1919) size (minute, small, moderate, large, or massive) and shape (rounded, nubbed, or pointed and tooth-like), and whether bifid
25) Baso-columellar lamella (BL) (none, weak, moderate, strong, very strong) and whether recessed
26) Baso-columellar tooth (BC): none, weak, small, moderate, large
27) Mid-columellar tooth (C) presence/absence, size (weak, small, moderate, large), and shape (description)
28) Upper-columellar tooth (UC) presence/absence, size (weak, small, moderate, large), and shape (description)
29) Baso-central tooth (B): (none, small, moderate, large) and whether recessed and concomitantly displaced toward the columella

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Umbilicus

30) Umbilicus: description

al barriers and/or shell sculpture or shell shape, also differed in both initial-whorl size (diameter of the first 1.5 whorls, 1%-13% minimum difference) and shell coiling tightness (whorls/ln height, 2%-16% minimum difference). The 7 pairs with indistinguishable apertural barriers and shell sculpture (Table 2) were diagnosed by their combinations of initial-whorl size (8%-30% minimum difference) and shell coiling tightness (0%-18% minimum difference).

Table 3 shows character variation in 11 of the most variable species, and the illustrations (Figs. 2-103) show some additional variant specimens not included in Table 3. Shell height can vary 40% or more within a species, depending primarily on the number of whorls achieved before maturity. Height/diameter varies up to 35%, apical angle 40%, sutural-depth and barreling indices 180% and 200% or more, embryonic whorl-count 17%, peristome height/width 33%, peristome width/shell diameter 40%, and lip width/peristome width 155%. The umbilicus can vary from imperforate to a crevice, and from a crevice to a very narrow well. Because of the great variabilities of these characters, I used them sparingly and cautiously, if at all, in diagnosing species.

Primary diagnostics among species were, in approximate descending order of importance, apertural barriers, body-whorl sculpture, initial-whorl size, shell coiling tightness, embryonic sculpture, apertural shape (when extreme); and sutural crenulation. Each apertural barrier can vary somewhat in size and, to a lesser extent, in shape, but its presence/absence, disposition, and size and shape relative to other barriers, are fairly constant within a species (Table 3). Rare presence/absence exceptions all involve the baso-columellar tooth: *Gulella zanaharyi* sp. nov. (Figs. 29, 69, 70), *G. fischerpiettei* sp. nov. (Figs. 32, 33), *G. satisfacta* (Figs. 34-38), and *G. ambalaniranae* (Figs. 71-74). Rare fixed-position exceptions involve the baso-central tooth's variable depth of recess, which, as I have interpreted it, may (Figs. 89-92) or may not (Figs. 76-78) correlate with displacement toward the columella.

Shell sculpture as seen in apertural view on the body and penultimate whorls, appears relatively stable within a species (Table 3). Sutural crenulation, although apparently independent of rib-sculpture in *Gulella* as it is in *Parvedentulina* Emberton and Pearce, 2000 (Emberton, in press b), sometimes produces faint subsutural impressions that I have discounted as rib sculpture. All species seem to show irregular growth lines, which I have ignored. Pre-apertural ribbing (Fischer-Piette *et al.*, 1994: figs. 60-62) seems ubiquitous within Madagascan *Gulella*, but I have not treated it here. Nor have I examined whether apical, post-embryonic ribbing differs from lower-whorl ribbing, except in the case of *Gulella ambanikelia* sp. nov., where the difference was extreme and unavoidably obvious.

The critical diagnostic roles of initial-whorl size (diameter of first 1.5 whorls) and shell coiling tightness (whorls/ln height) have already been demonstrated in Tables 2 and 4. In Table 3, within-species variation ranges about 1%-8% for both (up to 12% in subspeciated species). Thus, Table 3 reinforces my confidence in the stability and diagnostic value of these two indices.

Embryonic-shell sculpture can range from smooth to faintly ribbed or from smooth to a trace of sutural notches within a species. Other, more distinctive sculptures such as beaded or spirally grooved, however, seem consistent and diagnostic. Apertural shape in a few extreme cases was clearly diagnostic. I have also occasionally drawn on sutural crenulation for diagnosing both subspecies and species, as its variance seems relatively low (Table 3).

Table 4 compares subspecies or possible subspecies within six extremely variable species. Four of these species have what I deemed morphologically distinct subspecies that seem well isolated by uninhabitable savannah (*Gulella ambrensis* sp. nov., *G. benjamini* sp. nov.) or by impassable karstic ridges within Ankarana Reserve (*G. fischerpiettei* sp. nov., *G. satisfacta*). The other two species I did not divide into subspecies. The broad range of *G. antongilae* sp. nov. was recently continuous rainforest, and its aberrant shells from Soanierana-Ivongo may have resulted from abnormal growth conditions in exotic eucalypt forest and scrub. The aberrant Namoroka population of *G. vakinifia* sp. nov. could be due to character displacement by *G. celestinae* sp. nov.; variation of *G. vakinifia* sp. nov. within Bemaraha Reserve is nearly covered by its variation within the far-distant Namoroka Reserve, although the tightly and loosely coiled shells respectively of southern and northern Bemaraha, separated by the Beboka River, could possibly be subspecies.

KEY TO SPECIES AND SUBSPECIES

References are to published figures; see the Systematics section below for authors and dates of species.

1a. Apertural dentition limited to a small parietal tooth, coiling very loose (whorls/ln height 2.1-3.0) 2
1b. Apertural dentition of two or more teeth, coiling loose to very tight (whorls/ln height 3.1-5.4). 3

2a. Apex rounded, aperture wide, coiling looser (whorls/ln height 2.1) . . . . *G. microdon* Fischer-Piette *et al.* (1994): fig. 52
2b. Apex angular, aperture narrow, coiling tighter (whorls/ln height 3.0) . . . . *G. rubinsterni* Fischer-Piette *et al.* (1994): fig. 53

3a. Apertural dentition of parietal and palatal teeth only

Table 2. Coiling tightness, initial-whorl size, and other differences between similar pairs of species in sympatry and allopatry. Abbreviations: *ambr., ambrensis*; BCT, baso-columellar tooth present; CRBM, columellar recessed baffle massive; MnDiff, minimum difference between sympatric species; MWC, middle whorls constricted; PABAP, pre-apertural base angular in profile; PTIO, palatal tooth often with internal outlier; RCD, ribbing completely diminished between upper and lower sutures; RU, ribbing undiminished between upper and lower sutures; *sat., satisfacta*; #Sn, number of snails; #Sta, number of stations; UCTP, upper-columellar tooth present; WRA, whorls ribbed above.

				Whorls/ln(Height)		Diam 1st 1.5 Whorls		
Sp./ssp.	Station(s)	#Sta	#Sn	Range	MnDiff	Range	MnDiff	Other Diagnostics
masoalae	306,307,311,314[1]	4	7	3.28-3.35[3]		1.25-1.35		–
antongilae	295,300,303[2]	3	3	3.38-3.50[4]	1%	1.10-1.13	10%	–
antongilae	364,366,756,758	4	4	3.42-3.58		1.05-1.11		–
boucheti	218	1	1	3.57		1.36		–
boucheti	222	1	1	3.82	12%	1.35	13%	–
petitboucheti	223[5]	1	1	4.34		1.18		–
ankaranensis	554,564,570,571	4	4	4.89-5.07		0.75- 0.79		–
ankaranensis	558	1	4	5.02-5.12	5%	0.75- 0.79	8%	–
f. fischerpiettei	558	1	4	4.69-4.78		0.86- 0.90		–
f. fischerpiettei	803	1	1	4.59		0.88		–
ankaranensis	554,558,564,572	1	1	4.96-5.12		0.75- 0.79		–
ankaranensis	571	1	1	4.89	12%	0.78	18%	–
sat. charlesblanci	571	1	1	4.30		0.95		–
ankaranensis	554,558,570,571	4	6	4.89-5.12		0.75- 0.79		–
ankaranensis	564	1	1	5.07	18%	0.78	17%	–
sat. satisfacta	564	1	4	4.09-4.18		0.94- 0.95		–
sat. satisfacta	576,577	2	5	4.12-4.21		0.912-0.962		–
mahia	400	1	2	4.09-4.12		0.99 -1.025		–
mahia	239	1	1	4.07	4%	0.975	4%	–
ranomasina	239	1	2	4.22-4.26		0.925-0.932		MWC
ranomasina	238,240,241	3	7	4.28-4.40		0.875-0.925		MWC
mahia	400	1	2	4.09-4.12		0.99 -1.025		–
mahia	239	1	1	4.07	4%	0.975	11%	–
ambr. capdambri	238	1	1	3.92		1.100		–
ambr. capdambri	230,233	2	3	3.77-3.90		1.058-1.075		–
ambr. capdambri	230,233	2	3	3.77-3.90		1.058-1.075		–
ambr. capdambri	238	1	1	3.92	8%	1.100	13%	–
zanaharyi	238	1	1	4.28		0.962		CRBM,PABAP,PTIO
zanaharyi	239,241,400,404,407	5	10	3.93-4.15		0.975-1.025		CRBM,PABAP,PTIO
ambr. orangea	224	1	3	3.88-4.04		1.025-1.038		–
capmini	224	1	3	4.33-4.63	7%	0.950-1.000	2%	WRA
ambr. orangea	225	1	1	3.97		1.03		–
capmini	225	1	1	4.33	8%	1.08	5%	WRA
jaominai	401	1	1	3.94		0.938		—
jaominai	404	1	2	3.90-3.98	2%	0.912-0.925	6%	–
zanaharyi	404	1	2	4.06-4.08		0.988		CRBM,PABAP,PTIO
zanaharyi	238,239,241,400,407	5	9	3.93-4.28		0.962-1.025		CRBM,PABAP,PTIO
jaominai	401	1	1	3.94		0.938		–
gallorum	401	1	3	3.71-3.80	4%	1.225-1.312	23%	–
jaominai	404	1	2	3.90-3.98		0.912-0.925		–
gallorum	405[6]	1	2	3.82-3.90	0%	1.325	30%	–
marojejyae	649	1	1	3.34		1.16		RCD
michellae	649	1	1	3.96	16%	1.14	2%	RU,BCT
vakinifia	61,62,64	3	7	4.66-4.82		0.782-0.838		ribbed
vakinifia	74	1	2	4.93-5.01	2%	0.838-0.850	1%	ribbed
celestinae	74	1	6	4.67-4.81		0.818-0.842		smooth,UCTP

[1] juveniles also found at 294, 295, and 297. [2] also found at 283, 285, 294, 295, and 297. [3] n = 3. [4] n = 2. [5] also occurs at 222, where shell is virtually identical. [6] upslope from and only 20 m higher elevation than 404.

Table 3. Character variation within 11 especially variable species of Madagascan *Gulella*, based on extreme individuals. Characters as in Fig. 1 and in Table 1. Abbreviations: D1st1.5Wh, diameter of first 1.5 whorls (mm); EmbWhls, embryonic whorl count; *fischerp.*, *fischerpiettei*; fRibs, faint riblets; fSpiral, faint spiral grooves or striae; LipW/PsW, apertural-lip width/peristome width; m-l, moderate to large; massi, massive; md-lg, moderate to large; p-t, peg-like to triangular; pegTr-rdTr, peg-triangular to rounded-triangular; PsHt/Wdth, peristome height/width; PsW/ShD, peristome width/shell diameter; r-t, rounded to triangular; rct-rt, rectangular to rounded-triangular; rd-knTr, rounded to knobbed-triangular; rnd, rounded; sm, smooth; sNt, slightly notched; T, tooth; trStNt, smooth to trace of sutural notches; vStrong, very strong; Wh/lnHt, number of whorls divided by natural log of shell height (index of coiling tightness).

Species	n	Height	Ht/Diam	Whorls	Wh/lnHt	ApAngle	Barrel	SutDepth	SutCrenul
*ambrensis**	5*	5.8-6.8	2.1-2.5	6.5-7.4	3.7-4.0*	90-115	3.5-05.0	4.0-9.0	weak-strong*
antongilae	3	5.9-7.2	2.2-2.6	6.2-6.8	3.4-3.5	85-095	< 0-03.5	4.9-7.7	moderate
*benjamini**	3*	3.0-3.4	1.9-2.1	5.8-6.0	4.8-5.4*	85-100	2.5-03.4	5.6-9.8	weak
bobaombiae	3	4.0-4.2	2.5-2.7	6.8-7.2	4.9-5.1	85-115	< 0-03.6	3.9-5.8	strong
boucheti	2	5.7-7.5	2.1-2.6	6.2-7.7	3.6-3.8	95-120	7.0-09.1	1.2-1.8	strong
capmini	2	4.8	1.9-2.0	6.8-6.9	4.3	120	0.0-2.63	3.7-6.6	moderate
*fischerp.**	2*	4.0-4.7	2.3-2.6	6.4-7.3	4.6-4.7*	90-115	1.1-3.3	3.3-5.6	moderate
hafahafa	2	6.9-7.7	1.7-2.3	6.6-7.6	3.4-3.7	80-095	0.9-07.4	4.8-7.3	moderate
*satisfacta**	4*	4.7-5.8	2.4-2.8	6.7-7.2	4.1-4.3*	85-105	0-4.2	1.5-8.5	mod-strong*
vakinifia	3	3.5-4.9	2.1-2.8	6.2-7.6	4.6-5.0	80-085	2.2-05.8	4.6-7.7	strong
zanaharyi	2	5.3-6.9	2.2-2.7	6.7-8.3	4.0-4.3	100-105	2.4-5.1	1.3-3.6	moderate

Species	RibStrength	RibDimin	EmbWhls	D1st1.5Wh	EmbSculpt	PsHt/Wdth
*ambrensis**	none	–	1.8-2.1	1.03-1.17*	sm-trStNt	1.0-1.1
antongilae	none	–	1.9-2.0	1.08-1.11	smooth	1.0-1.2
benjamini	moderate	none	1.8-2.1	0.73-0.79	sm-fRibs	1.0
bobaombiae	none	–	2.0-2.2	0.74-0.79	smooth	1.0-1.1
boucheti	none	–	1.6-1.7	1.35-1.36	fSpiral	1.0-1.1
capmini	moderate	complete	2.1-2.2	1.00-1.08	smooth	0.8-0.9
*fischerp.**	none	–	1.9-2.0	0.80-0.90*	smooth	1.0
hafahafa	strong	none	2.1	1.00-1.03	beaded	1.2
*satisfacta**	none-weak*	none	2.1	0.91-0.95	smooth	0.9-1.2
vakinifia	strong	none	1.8-2.1	0.78-0.80	sm-fRibs	1.1-1.4
zanaharyi	none	–	1.8-2.0	0.93-0.99	smooth	1.0-1.1

Species	PsW/ShD	LipW/PsW	ParietalT	PalatalTooth	Par-PalEmbayment
*ambrensis**	0.7	0.14-0.22	large-mod*	large, triang	mod wide
antongilae	0.6	0.11-0.14	small	sm-md, rct-rt	wide
benjamini	0.6-0.7	0.17-0.20	moderate	md-lg, tr-pegTr	wide
bobaombiae	0.7-0.8	0.19-0.26	large	lg, triang-pegTr	mod wide
boucheti	0.7	0.18-0.21	moderate	md, rnd-squared	mod wide
capmini	0.7	0.15-0.19	moderate	large, rd-knTr	mod wide
*fischerp.**	0.7	0.16-0.23	large-mod*	large, triang	mod wide
hafahafa	0.5-0.7	0.24-0.34	lg-massi	lg-massi, bifid	narrow-mod wide
*satisfacta**	0.7	0.16-0.23	large	lg, pegTr-rdTr	mod wide
vakinifia	0.6-0.7	0.11-0.28	massi, sNt	massive, bifid	narrow
zanaharyi	0.6-0.7	0.20	lg-massive	lg-vLg, triang	fairly narrow

Species	Baso-CentT	Baso-ColLamella	Baso-ColT	Mid-ColT	Upp-ColT	ColRecBaffle
*ambrensis**	none	strong	none	none	none	moderate
antongilae	none	none	none	none	none	minute
benjamini	none	none	none	m-l, r-t	none	small
bobaombiae	none	moderate	small-mod	none	none	moderate
boucheti	none	none	none	none	none	minute
capmini	none	strong	none	none	none	moderate
*fischerp.**	none	moderate	no-weak*	none	none	small-modera*
hafahafa	small-mod	none	none	m-l, p-t	peg-like	small
*satisfacta**	none	strong-vStrong*	none	wk-none*	none	small
vakinifia	small-lg	moderate	none	m-l, rnd	none	moderate
zanaharyi	none	mod-stg, recess	none-mod	none	none	massive

Species	Umbilicus
*ambrensis**	crevice
antongilae	imperf-crevice
benjamini	crevice
bobaombiae	tiny crevice
boucheti	imperf-minute crevice
capmini	crevice
*fischerp.**	imperf-crevice
hafahafa	crevice-very narrow well
*satisfacta**	imperf-crevice
vakinifia	crevice-very narrow well
zanaharyi	small crevice

*divided into subspecies (see Table 4).

(although the columellar recessed baffle can resemble a tooth) 4

3b. Apertural dentition of parietal and palatal teeth and at least one other tooth 51

4a. Parietal and palatal teeth minute and approximately equal in size, shell height less than 4.5 mm (whorls/ln height 4.5), moderately strong rib sculpturing . . . . *G. nifikelia* Fig. 2

4b. Parietal and palatal teeth small to large and generally unequal in size, if small and approximately equal then shell height is greater than 6.5 mm (whorls/ln height 3.4) and rib sculpture is very weak 5

5a. Coiling loose (whorls/ln height 3.1-3.5), shell sculpture smooth or nearly so (but with a crenulate suture), parietal tooth small, parieto-palatal embayment wide. 6

5b. Coiling moderate to tight (whorls/ln height 3.6-5.4), or, if loose (whorls/ln height 3.1-3.5), shell sculpture moderately to strongly ribbed, parietal tooth moderate to large, parieto-palatal embayment narrow to moderate in width 8

6a. Coiling looser (whorls/ln height 3.1), Antalaha region northeast of Masoala Peninsula . . . . *G. bouchardi* Fischer-Piette *et al.* (1994): plate V fig. 1

6b. Coiling tighter (whorls/ln height 3.3-3.5), western Masoala Peninsula and southwest of it 7

7a. Diameter of first 1.5 whorls about 1.3 mm, coiling generally looser (whorls/ln height about 3.3-3.4), western Masoala Peninsula . . . . *G. masoalae* Fig. 3

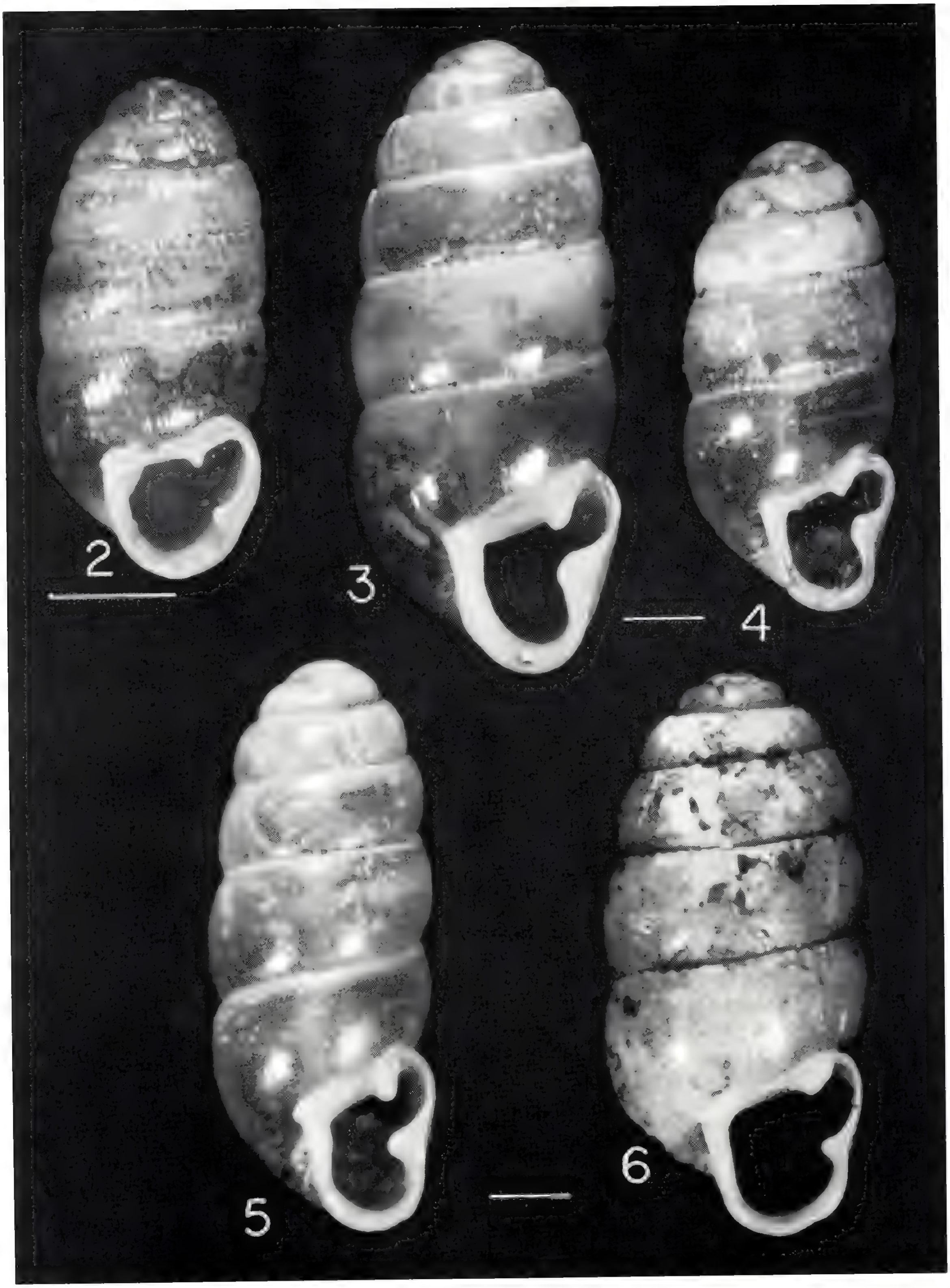
7b. Diameter of first 1.5 whorls about 1.1 mm, coiling generally tighter (whorls/ln height about 3.4-3.6), western Masoala Peninsula and southwest of it . . . . *G. antongilae* Figs. 4, 5, 6

8a. Columellar recessed baffle only shallowly recessed and nubbed or bifid like a third tooth; shell cylindrical, smooth, without sutural crenulation; parietal tooth smallish and sometimes weakly bifid; palatal tooth smaller and shaped like a rounded nub or peg;

Table 4. Coiling tightness, initial-whorl size, and other differences among subspecies and possible subspecies. Abbreviations: ATVS, apertural teeth very small; BCLM, baso-columellar lamella massive and extending upward to near the columellar insertion; +c, sympatric with *Gulella celestinae*; -c, allopatric from *G. celestinae*; CWRS, continuous, weak rib sculpture; D1st1.5Wh, diameter of the first 1.5 whorls; DF, deciduous forest; EFS, eucalypt (exotic) forest and scrub; MCT, mid-columellar tooth present; PT+R, palatal tooth recessed to not recessed; PTLLE, palatal tooth lamellar all the way to the apertural-lip edge; PTLSBLE, palatal-tooth lamella stops before the apertural-lip edge; RF, rainforest; SCS, sutural crenulation strong; SCW, sutural crenulation weak; #Sn, number of snails; #Sta, number of stations; Wh/lnHt, shell whorls divided by the natural logarithm of shell height.

Species/Subspec.	Locality	#Sta	#Sn	Wh/lnHt	D1st1.5Wh	Other Differences
antongilae	W. Masoala	3	3	3.38-3.50[1]	1.10-1.13	RF
antongilae	Mananara	1	1	3.45	1.11	RF
antongilae	Ambatovaky	2	2	3.42-3.58	1.05- 1.06	RF
antongilae	Soanierana	2	3	3.38[2]	1.08- 1.18	EFS,ATVS
antongilae	IsleSteMarie	1	1	3.48	1.10	RF
f. fischerpiettei	Ankarana	2	5	4.59-4.78	0.86- 0.90	–
f. enigma	Ankarana	2	4	4.58-4.71	0.80- 0.84	–
s. satisfacta	Ankarana	3	9	4.09-4.21	0.913-0.962	–
s. charlesblanci	Ankarana	1	1	4.30	0.950	MCT
s. vitsia	Ankarana	1	1	4.18	0.950	CWRS,BCLM
a. ambrensis	Mt. d'Ambre	2	8	3.79-3.97	1.025-1.050	PTLSBLE,SCW,RF
a. andavakoerae	Andavakoera	2	2	3.68-3.90	1.075-1.100	PTLLE,SCS,DF
a. capdambri	Cap d'Ambre	2	4	3.77-3.92	1.058-1.100	PTLSBLE,SCS,PT+R,DF
a. orangea	Cap Mine	2	4	3.88-3.98	1.025-1.038	PTLSBLE,SCS,DF
a. rakotomalalai	Analamera	2	2	3.76-3.87	1.150-1.168	PTLLE,SCS,DF
b. benjamini	Vohimena Mts	2	2	4.8- 4.9	0.73- 0.79	–
b. saintelucensis	ForêtSteLuce	1	1	5.4	0.78	–
vakinifia	S. Bemaraha	1	4	4.99-5.13	0.775-0.838	–
vakinifia	N. Bemaraha	1	3	4.45-4.64	0.800-0.812	–
vakinifia	Namoroka -c	3	7	4.66-4.82	0.782-0.838	–
vakinifia	Namoroka +c	1	2	4.93-5.01	0.838-0.850	–

[1] n = 2. [2] n = 1.



Figs. 2-6. Fig. 2. *Gulella nifikelia* sp. nov. holotype, Manombo Reserve. Fig. 3. *G. masoalae* sp. nov. holotype, western Masoala Peninsula. Figs. 4-6. *G. antongilae* sp. nov.: Fig. 4 holotype, western Masoala Peninsula; Figs. 5, 6 paratypes: Fig 5 southwest of Mananara; Fig. 6 exotic eucalypt forest, Soanierana Ivongo. All scale bars 1 mm.

parietal-palatal embayment wide 9

8b. Otherwise 10

9a. Shell smaller for the same number of whorls (whorls/ln height about 3.9), diameter of first 1.5 whorls about 0.9 mm . . . . *G. andreana* Fig. 7

9b. Shell larger for the same number of whorls (whorls/ln height about 3.6), diameter of first 1.5 whorls about 1.1 mm . . . . *G. beandreana* Figs. 8, 9

10a. Parietal tooth deeply recessed, aperture constricted centrally into an hourglass shape . . . . *G. constricta* Fig. 10

10b. Parietal tooth not recessed, aperture constricted slightly if at all 11

11a. Baso-columellar lamella absent to weak 12

11b. Baso-columellar lamella moderate to strong 30

12a. General rib sculpture weak to none 13

12b. General rib sculpture strong to moderate 24

13a. Aperture roughly triangular, parietal tooth bifid . . . . *G. ambatovakiae* Fig. 12

13b. Aperture rounded to ovate, parietal tooth undivided 14

14a. Diameter of first 1.5 whorls about 1.5 mm, height generally greater than 11 mm . . . . *G. magnifica* Fig. 11

14b. Diameter of first 1.5 whorls 1.3 mm or less, height less than 9.5 mm 15

15a. Rib sculpture weak but conspicuous, shell tall (height/diameter 2.8 or greater) and cylindrical to columnar 16

15b. Rib sculpture absent or weak and inconspicuous, shell stouter (height/diameter 2.6 or less) and barreled to slightly columnar 17

16a. Diameter of first 1.5 whorls 1.0-1.1 mm . . . . *G. pseudandreana* Fig. 13

16b. Diameter of first 1.5 whorls 1.2-1.3 mm . . . . *G. gallorum* Fig. 14

17a. Parietal and palatal teeth very large, columellar recessed baffle conspicuous . . . . *G. rakotoarisoni* Fig. 15

17b. Parietal and palatal teeth moderate, columellar recessed baffle inconspicuous or not visible in apertural view 18

18a. Diameter of first 1.5 whorls 1.2-1.4 mm; palatal tooth low, broad, and squarish; sutures shallowly impressed; embryonic whorls 1.6 to 1.7 19

18b. Diameter of first 1.5 whorls 0.8-1.0 mm; palatal tooth elevated, narrow, and triangular or pegged; sutures moderately impressed; embryonic whorls 1.8 to 2.2 20

19a. Diameter of first 1.5 whorls about 1.4 mm; whorls descending more rapidly (whorls/ln height about 3.6-3.8) . . . . *G. boucheti* Figs. 16, 17

19b. Diameter of first 1.5 whorls about 1.2 mm; whorls descending more slowly (whorls/ln height about 4.3) . . . . *G. petitboucheti* Fig. 18

20a. Tighter coiling (whorls/ln height about 4.4-4.7) 21

20b. Looser coiling (whorls/ln height about 4.0-4.3). . . . 23

21a. Diameter of first 1.5 whorls about 0.95 mm; sutural crenulation weak; southeasternmost Madagascar . . . . *G. reeae* Fig. 19

21b. Diameter of first 1.5 whorls about 0.80-0.81 mm; sutural crenulation strong; central to south-central Madagascar 22

22a. Looser coiling (whorls/ln height about 4.5); aperture proportionally smaller (aperture width/shell diameter 0.5); south-central eastern rainforest . . . . *G. miaranoniae* Fig. 20

22b. Tighter coiling (whorls/ln height about 4.7); aperture proportionally larger (aperture width/shell diameter 0.7); central western semi-deciduous forest . . . . *G. bebokae* Fig. 21

23a. Looser coiling (whorls/ln height about 4.0); diameter of first 1.5 whorls 0.9-1.0 mm; Manakara region (Fotobohitra) . . . . *G. fotobohitrae* Fig. 22

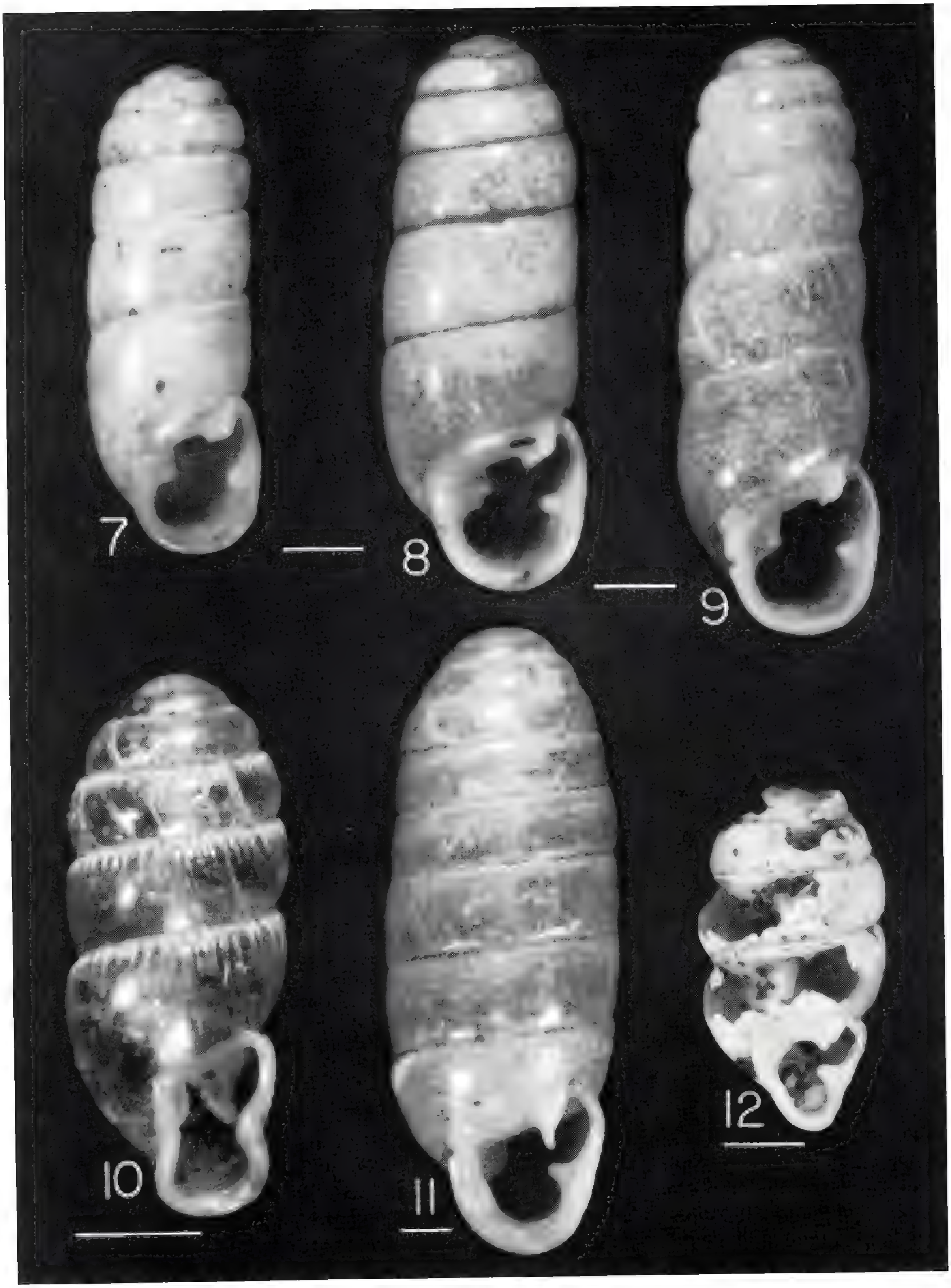
23b. Tighter coiling (whorls/ln height about 4.2-4.3); diameter of first 1.5 whorls about 0.8 mm; Tamatave region (Betampona Reserve) . . . . . *G. razafyi* Fig. 23

24a. Shell height generally greater than 9 mm: looser coiling (whorls/ln height about 3.2-3.4) 25

24b. Shell height generally less than 7.5 mm: tighter coiling (whorls/ln height about 3.7-4.4) 26

25a. Looser coiling (whorls/ln height about 3.2), middle whorls with flattened peripheries . . . . *G. josephinae* Fig. 24

25b. Tighter coiling (whorls/ln height about 3.4), middle whorls with rounded peripheries . . . .*G. soulaiana* Fischer-Piette *et al.* (1994): plate IV fig. 19



Figs. 7-12. Fig. 7. *Gulella andreana* Fischer-Piette, Blanc and Vukadinovic, 1974, specimen, Ranomafana National Park. Figs. 8, 9. *G. beandreana* sp. nov.: Fig. 8 holotype, Manombo Reserve; Fig. 9 paratype, Mount Ambalanirana. Fig. 10. *G. constricta* sp. nov. holotype, Tsaratanana Reserve. Fig. 11. *G. magnifica* sp. nov. holotype, Ankarana Reserve. Fig. 12. *G. ambatovakiae* sp. nov. holotype, Ambatovaky Reserve. All scale bars 1 mm.

26a. General rib sculpture very strong and high-standing; Ankarana Reserve and vicinity 27
26b. General rib sculpture moderately strong and low-standing; elsewhere than Ankarana Reserve 28

27a. Looser coiling (whorls/ln height about 3.7); larger initial whorl (diameter of first 1.5 whorls about 1.0 mm) . . . . *G. rugosa* Fig. 25
27b. Tighter coiling (whorls/ln height about 4.1); smaller initial whorl (diameter of first 1.5 whorls about 0.8 mm) . . . . *G. columna* Fig. 26

28a. Palatal tooth high in position and notched opposite the parietal tooth; tighter coiling (whorls/ln height 4.5-4.6). . . . . *G. pearcei* Fig. 27
28b. Palatal tooth medial in position and unnotched; looser coiling (whorls/ln height 4.1-4.4). 29

29a. Looser coiling (whorls/ln height about 4.1); rainforest in north-central Madagascar . . . . *G. tsaratananae* Fig. 28
29b. Tighter coiling (whorls/ln height about 4.4); dry forest in southwestern Madagascar . . . . *G. miaryi* Fischer-Piette *et al.* (1994): fig. 54

30a. General rib sculpture weak to none 31
30b. General rib sculpture strong to moderate 46

31a. Columellar recessed baffle huge, pre-apertural base angular in profile, palatal tooth massive and often with deeply internal outlier . . . . *G. zanaharyi* Figs. 29, 69, 70
31b. Columellar recessed baffle small to moderate, pre-apertural base rounded in profile, palatal tooth moderate to large and without a deeply internal outlier 32

32a. Diameter of first 1.5 whorls about 1.3 mm; palatal tooth transverse; parietal tooth joined to and continuous with the apertural lip . . . . *G. lohabea* Fig. 30
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33b. Looser coiling (whorls/ln height 3.7-4.4) 36

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34b. Looser coiling (whorls/ln height 4.6-4.8); diameter of first 1.5 whorls 0.80-0.90 mm 35

35a. Diameter of first 1.5 whorls 0.86-0.90 mm; palatal tooth nub-like and slightly recessed; parietal tooth separated by a groove from the apertural lip . . . . *G. fischerpiettei s.s.* Fig. 32
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38a. Whorls/ln height 4.3; small baso-columellar tooth present . . . . *G. satisfacta charlesblanci* Fig. 34
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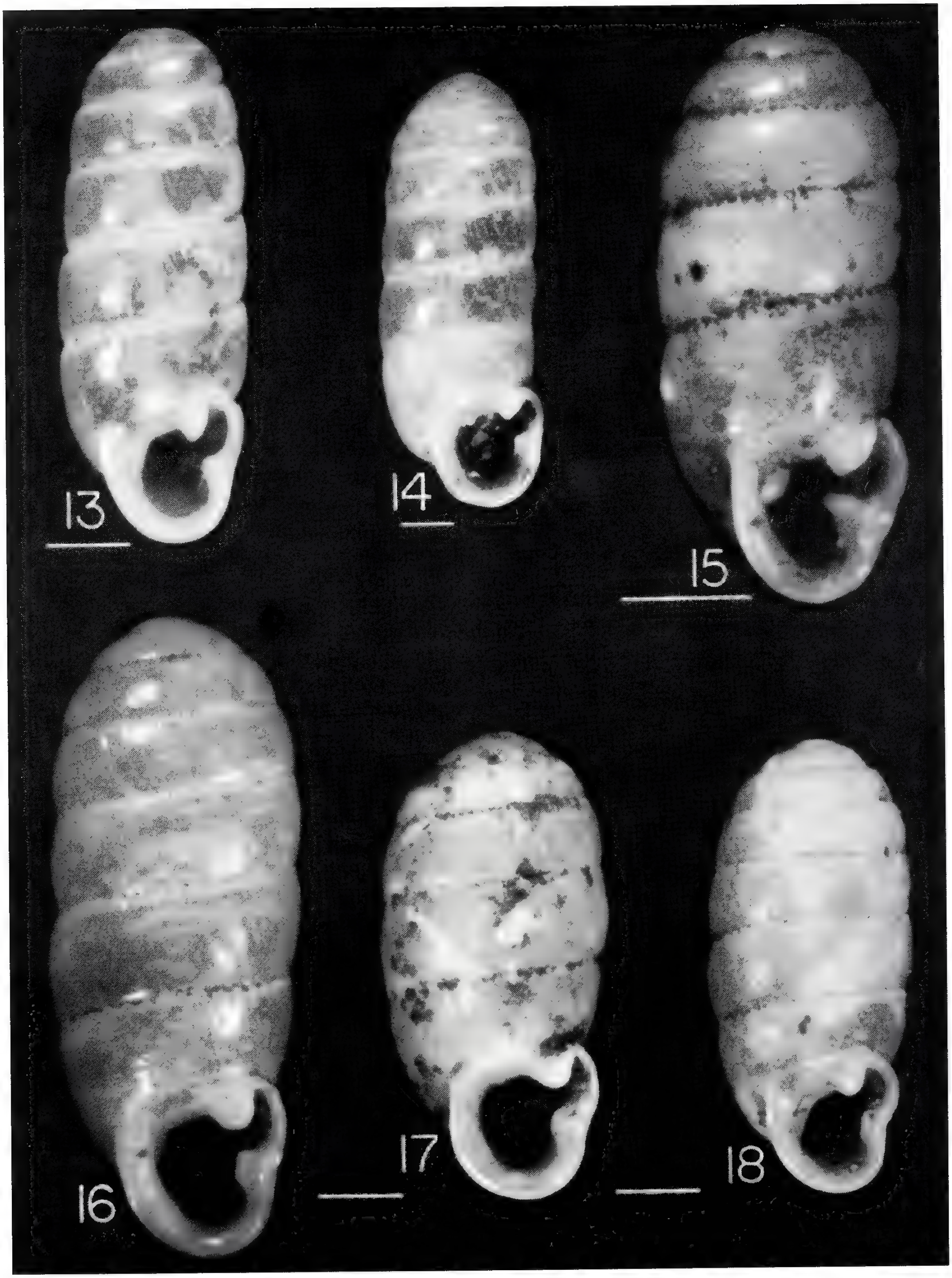
44a. Diameter of first 1.5 whorls 1.075-1.100 mm; Andavakoera massif . . . .



Figs. 13-18. Fig. 13. *Gulella pseudandreana* sp. nov. holotype, Bemaraha Reserve. Fig. 14. *G. gallorum* Fischer-Piette, Blanc and Salvat, 1975, specimen, Cap d'Ambre. Fig. 15. *G. rakotoarisoni* sp. nov. holotype, Ankarana Reserve. Figs. 16, 17. *G. boucheti* Fischer-Piette, Blanc, Blanc and Salvat, 1994, specimens: Fig. 16 type locality, Montagne des Français; Fig. 17 Montagne des Orchides. Fig. 18. *G. petitboucheti* sp. nov. holotype, Montagne des Français. All scale bars 1 mm.

. . . .*G. ambrensis andavakoerae* Fig. 44

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46a. General rib sculpture continuing undiminished from upper to lower suture 47

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47b. Palatal tooth a short spiral lamella that is triangular in apertural view; tighter coiling (whorls/ln height about 3.85); larger initial whorl (diameter of first 1.5 whorls about 1.3 mm) . . . . *G. nakamaroa* Fig. 50

48a. Columellar recessed baffle conspicuous, nubbed, and toothlike; palatal tooth recessed about as deeply as the recessed columellar baffle . . . . *G. capmini* Figs. 48, 51

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49a. Shell large and loosely coiled (whorls/ln height about 3.3-3.4, diameter of first 1.5 whorls 1.0-1.1 mm) . . . .*G. marojejyae* Fig. 52

49b. Shell small and tightly coiled (whorls/ln height about 4.1-4.6, diameter of first 1.5 whorls 0.8-0.9 mm) 50

50a. Loose coiling (whorls/ln height about 4.1-4.2); large parietal tooth; deciduous-forest habitat . . . . *G. griffithsi* Fig. 53

50b. Tight coiling (whorls/ln height about 4.5-4.6); small parietal tooth; rainforest habitat . . . . *G. tsara* Fig. 54

51a. General rib sculpture extremely dense . . . . *G. microstriata* Fig. 55

51b. General rib sculpture, when present, moderately dense 52

52a. General rib sculpture weak to none 53

52b. General rib sculpture strong to moderate 67

53a. Shell extremely minute (whorls/ln height about 5.4); no evident sutural crenulation . . . . *G. kelibea* Fig. 56

53b. Shell larger (whorls/ln height about 3.6-5.0); moderate to strong sutural crenulation 54

54a. Shell shape steeply pyramidal; whorls/ln height about 3.6; an introduced species found only in gardens and settlements. . . . .*G. bicolor* Fischer-Piette *et al.* (1994): fig. 50

54b. Shell shape barreled to columnar; whorls/ln height about 3.7-5.0; native species not known from gardens or settlements 55

55a. Loose coiling (whorls/ln height about 3.7-3.8); initial whorl generally larger (diameter of first 1.5 whorls 1.0-1.2 mm) 56

55b. Tight coiling (whorls/ln height about 4.0-5.0); initial whorl generally smaller (diameter of first 1.5 whorls 0.8-1.0 mm) 57

56a. Narrow baso-columellar tooth; upper-columellar tooth often present; tighter coiling (whorls/ln height about 3.8); smaller initial whorl (diameter of first 1.5 whorls about 1.0-1.1 mm) . . . *G. analamerae* Fig. 57

56b. Broad baso-columellar tooth; never an upper-columellar tooth; looser coiling (whorls/ln height about 3.7); larger initial whorl (diameter of first 1.5 whorls about 1.2 mm) . . . . *G. vohimarae* Fig. 58

57a. Mid-columellar tooth present, baso-columellar tooth absent (but its position may be approached by the mid-columellar tooth). 58

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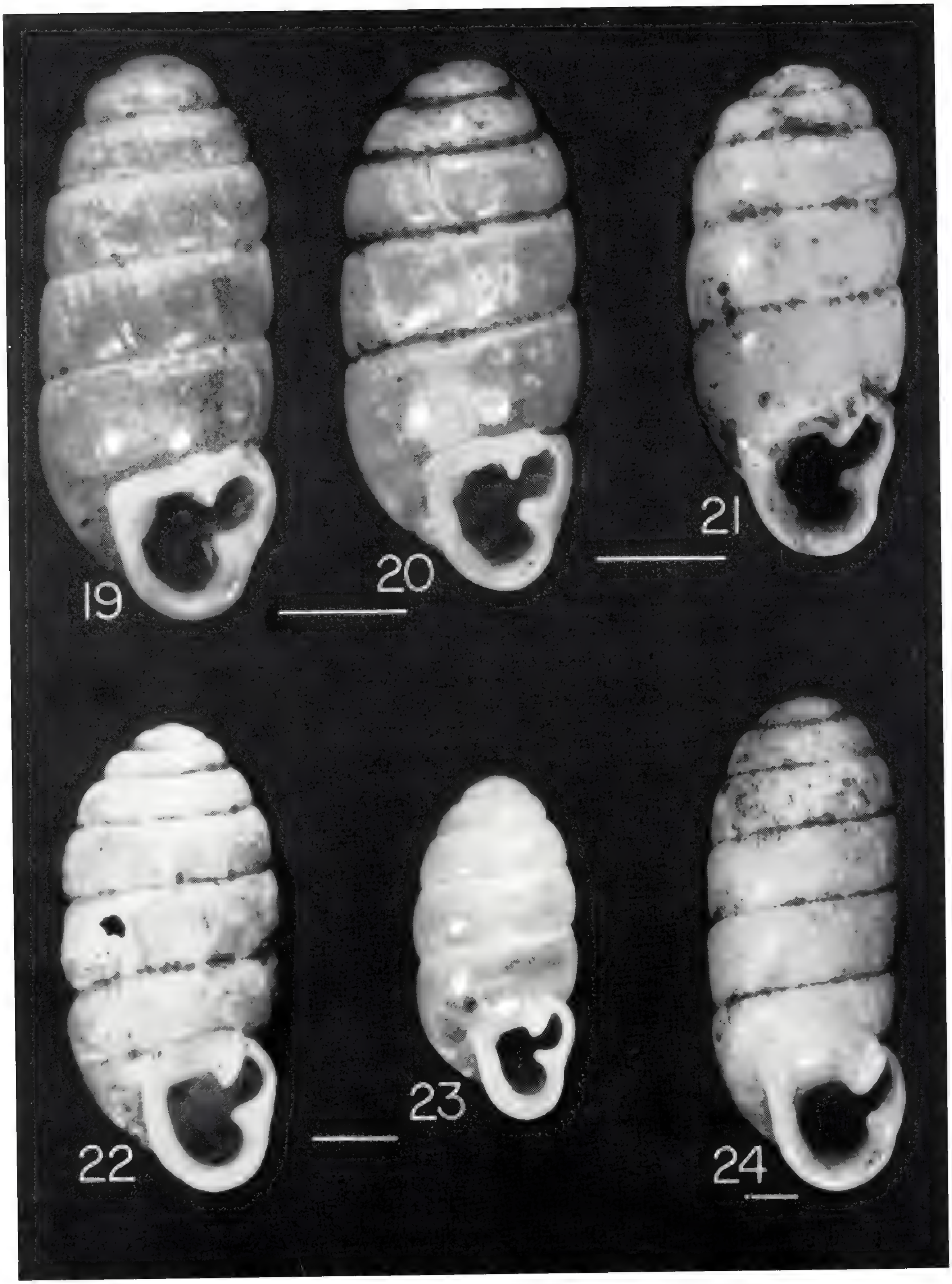
58a. Shell stout and loosely coiled (whorls/ln height about 4.3, diameter of first 1.5 whorls about 0.9); outer edge of peristome not conspicuously constricted . . . . *G. nosybei* Fig. 61

58b. Shell slender and tightly coiled (whorls/ln height about 4.7-4.8, diameter of first 1.5 whorls about 0.8); outer edge of peristome conspicuously constricted 59

59a. No upper-columellar tooth; parietal and palatal teeth not conspicuously bifid . . . . *G. tendronia* Fig. 59

59b. Upper-columellar tooth present; parietal and palatal teeth conspicuously bifid. . . . . . *G. celestinae* Fig. 60

60a. Palatal and columellar sides of the peristome straight,



Figs. 19-24. Fig. 19. *Gulella reeae* Emberton and Pearce, 2000, holotype, south of Andohahela Reserve. Fig. 20. *G. miaranoniae* sp. nov. holotype, eastern Ranomafana National Park. Fig. 21. *G. bebokae* sp. nov. holotype, Bemaraha Reserve. Fig. 22. *G. fotobohitrae* sp. nov. holotype, east of Ranomafana National Park. Fig. 23. *G. razafyi* sp. nov. holotype, Betampona Reserve. Fig. 24. *G. josephinae* sp. nov. holotype, Namoroka Reserve. All scale bars 1 mm.

parallel, and slanted conspicuously inward toward the columella; whorls/ln height 4.4-4.5 and apical, post-embryonic whorls smooth 61

60b. Palatal and columellar sides of the peristome curved, non-parallel, and not slanted conspicuously inward; if whorls/ln height 4.4-4.5, then apical, post-embryonic whorls ribbed 62

61a. Palatal tooth notched to receive the parietal tooth and inwardly slanting downward; northern Cap d'Ambre . . . . *G. bemoka* Fig. 62

61b. Palatal tooth unnotched and not inwardly slanting downward; Analamera Reserve . . . . *G. vavakelia* Fig. 63

62a. Baso-columellar tooth large and buttressed more strongly above than below, palatal tooth slightly bifid . . . . *G. mitsikia* Fig. 64

62b. Baso-columellar tooth moderate and buttressed equally above and below, palatal tooth undivided 63

63a. Shell small and tightly coiled (whorls/ln height 4.9-5.1, diameter of first 1.5 whorls 0.7-0.8 mm) . . . . *G. bobaombiae* Figs. 65-67

63b. Shell larger and more loosely coiled (whorls/ln height 4.0-4.4, diameter of first 1.5 whorls 0.9-1.0 mm) 64

64a. Apical, post-embryonic whorls weakly but quite noticeably ribbed; baso-columellar tooth a distinct knob . . . . *G. ambanikelia* Fig. 68

64b. Apical, post-embryonic whorls without noticeable rib sculpture; baso-columellar tooth broad and less distinct 65

65a. Columellar recessed baffle huge, pre-apertural base angular in profile, palatal tooth massive and often with deeply internal outlier; Cap d'Ambre . . . . *G. zanaharyi* Figs. 29, 69, 70

65b. Columellar recessed baffle small to moderate, pre-apertural base rounded in profile, palatal tooth moderate to large and without a deeply internal outlier; Ankarana Reserve. 66

66a. Tight coiling (whorls/ln height 4.6-4.8) . . . . *G. fischerpiettei* Figs. 32, 33

66b. Loose coiling (whorls/ln height 4.1-4.3) . . . . *G. satisfacta* Figs. 34-38

67a. General rib sculpture diminishing almost completely toward the lower suture 68

67b. General rib sculpture diminishing little to none toward the lower suture 70

68a. Palatal tooth undivided and unnotched; shell large and loosely coiled (whorls/ln height about 3.8-3.9); baso-columellar tooth broad and indefinite . . . . *G. ambalaniranae* Figs. 71-74

68b. Palatal tooth bifid or notched; shell smaller and more tightly coiled (whorls/ln height about 4.2-4.9); baso-columellar tooth narrower and clearly defined. . . . 69

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69b. Mid-columellar and baso-central teeth present and massive; no baso-columellar tooth; parietal and palatal teeth notched and interlocking; shell much larger and more loosely coiled (whorls/ln height about 4.2) . . . . *G. mihomehia* Figs. 76-78

70a. Palatal tooth undivided and unnotched 71

70b. Palatal tooth bifid or with a secondary node 78

71a. No mid-columellar tooth; basal and columellar dentition limited to a single broad baso-columellar tooth 72

71b. Mid-columellar tooth present; baso-columellar tooth, if present, small and narrow 73

72a. Shell small and tightly coiled (whorls/ln height about 4.6-4.7, diameter of first 1.5 whorls about 0.75 mm); general rib sculpture strong; unique embryonic sculpture of minute riblets and two subsutural spiral grooves . . . . *G. manomboae* Fig. 79

72b. Shell larger and more loosely coiled (whorls/ln height about 4.0, diameter of first 1.5 whorls about 1.15 mm); general rib sculpture moderate in strength; embryonic sculpture smooth . . . *G. michellae* Fig. 80

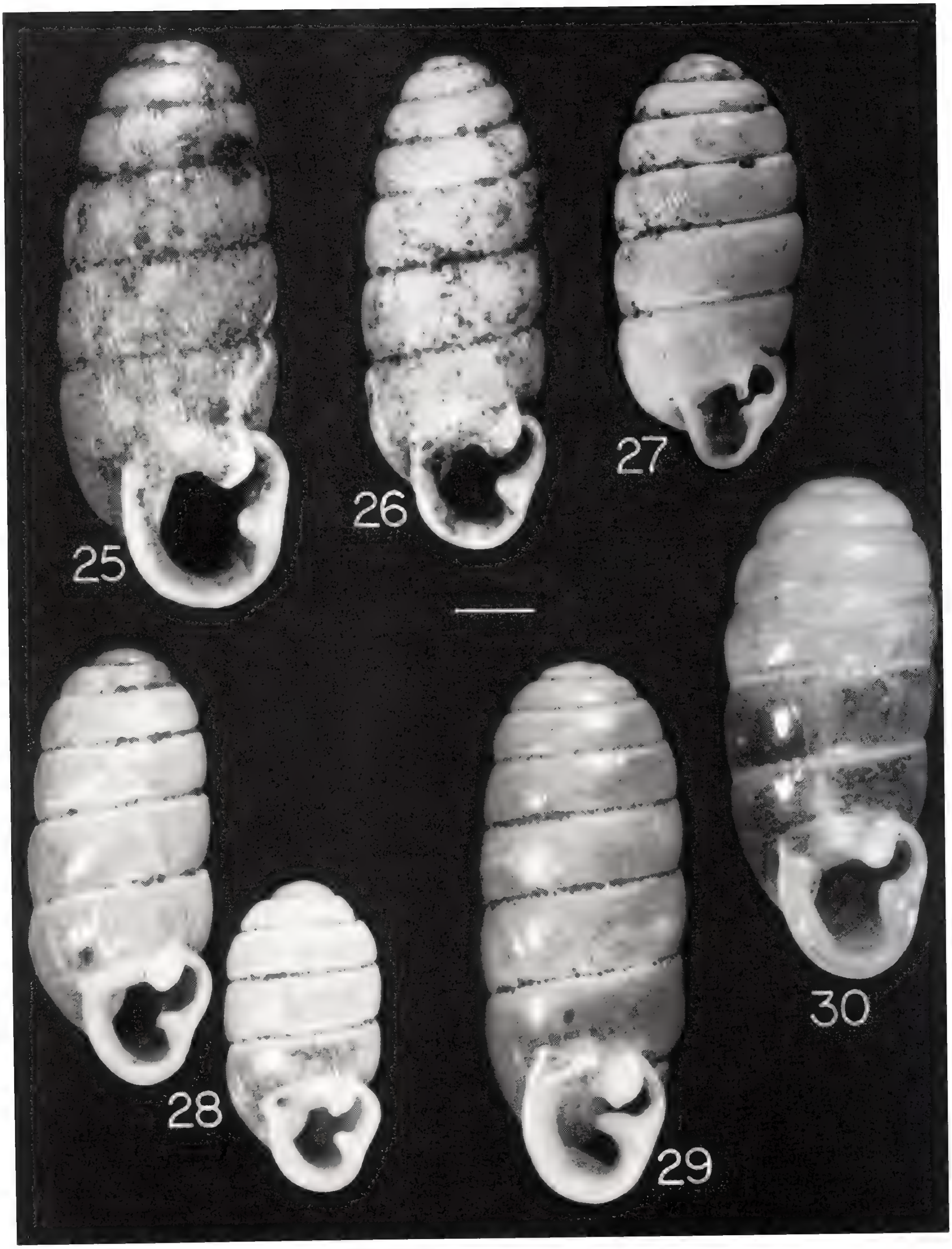
73a. Columellar recessed baffle enormous; baso-central and mid-columellar teeth both present; shell large and loosely coiled (whorls/ln height about 3.8) . . . . *G. mahagaga* Fig. 81

73b. Columellar recessed baffle small to moderate; no baso-central tooth; shell smaller and more tightly coiled (whorls/ln height about 4.0-4.9) 74

74a. Shell small and tightly coiled (whorls/ln height 4.8-5.5) 75

74b. Shell large and loosely coiled (whorls/ln height about 4.0-4.1) 77

75a. Mid-columellar tooth connected at its base to both upper columellar and baso-columellar teeth; Marojejy Reserve (northeastern Madagascar). . . . .



Figs. 25-30. Fig. 25. *Gulella rugosa* sp. nov. holotype, Ankarana Reserve. Fig. 26. *G. columna* sp. nov. holotype, Ankarana Reserve. Fig. 27. *G. pearcei* sp. nov. holotype, Montagne des Français. Fig. 28 (two shells). *G. tsaratananae* sp. nov.: larger shell holotype, smaller shell paratype, Tsaratanana Reserve. Fig. 29. *G. zanaharyi* sp. nov. holotype, northern Cap d'Ambre. Fig. 30. *G. lohabea* sp. nov. holotype, Analamera Reserve. Scale bar 1 mm.

. . . . *G. hafa* Fig. 82

75b. Mid-columellar tooth isolated, no upper columellar or baso- columellar tooth present; extreme southeastern Madagascar 76

76a. Shell larger and more loosely coiled (whorls/ln height 4.8-4.9); montane forests . . . . *G. benjamini s.s.* Figs. 83-84

76b. Shell smaller and more tightly coiled (whorls/ln height 5.4); coastal forests . . . . *G. benjamini saintelucensis* Fig. 85

77a. Columella slanted conspicuously outward; palatal tooth smallish; near Andringitra Reserve (southeastern Madagascar). . . . . *G. lubeti* Fischer-Piette *et al.* (1994): fig. 63

77b. Columella nearly vertical; palatal tooth very large; Marojejy and Ambatovaky Reserves (northeastern Madagascar) . . . . *G. mahafinaratra* Figs. 86-88

78a. Both upper- and mid-columellar teeth present; shell large and loosely coiled (whorls/ln height 3.4-3.7); unique, beaded embryonic sculpture . . . . *G. hafahafa* Figs. 89-92

78b. Either upper- or mid-columellar tooth may be present, but not both; shell smaller and more tightly coiled (whorls/ln height 4.3-4.9); smooth to ribbed embryonic sculpture 79

79a. Strongly ribbed embryonic sculpture; palatal and mid-columellar teeth point directly to each other; no baso-central or baso-columellar tooth . . . . *G. vatosoa* Fig. 93

79b. Smooth to trace-ribbed embryonic sculpture; palatal and mid-columellar teeth do not point directly to each other; a baso-central or baso-columellar tooth present 80

80a. Recessed baso-central tooth present; no baso-columellar tooth; parietal tooth slightly bifid and not entering directly into palatal-tooth notch . . . . *G. vakinifia* Figs. 94-97

80b. No baso-central tooth; recessed baso-columellar tooth present; parietal tooth undivided and entering directly into palatal-tooth. 81

81a. Upper-columellar tooth present; shell coiling tighter (whorls/ln height about 4.4-4.5); Montagne des Orchides, southeast of Diego Suarez . . . . *G. orchida* Figs. 98, 99

81b. No upper-columellar tooth; shell coiling looser (whorls/ln height about 4.2-4.3); southern Cap d'Ambre . . . . *G. magnorchida* Fig. 100

SYSTEMATICS

Higher classification follows Nordsieck (1986). Type and voucher materials are placed in the Florida Museum of Natural History, University of Florida, Gainesville (UF); the Australian Museum, Sydney (AMS); the Academy of Natural Sciences of Philadelphia (ANSP); and the Muséum national d'Histoire naturelle, Paris (MNHN), which does not assign catalog numbers to its types.

Class GASTROPODA
Subclass PULMONATA
Order STYLOMMATOPHORA
Superfamily STREPTAXOIDEA
Family STREPTAXIDAE Gray, 1860
Genus *Gulella* Pfeiffer, 1856
(*sensu* Fischer-Piette *et al.*, 1994,
who separate *Gonospira* Swainson, 1840)

Gulella microdon (Morelet, 1860)
Fischer-Piette *et al.* (1994): fig. 52 (specimen)

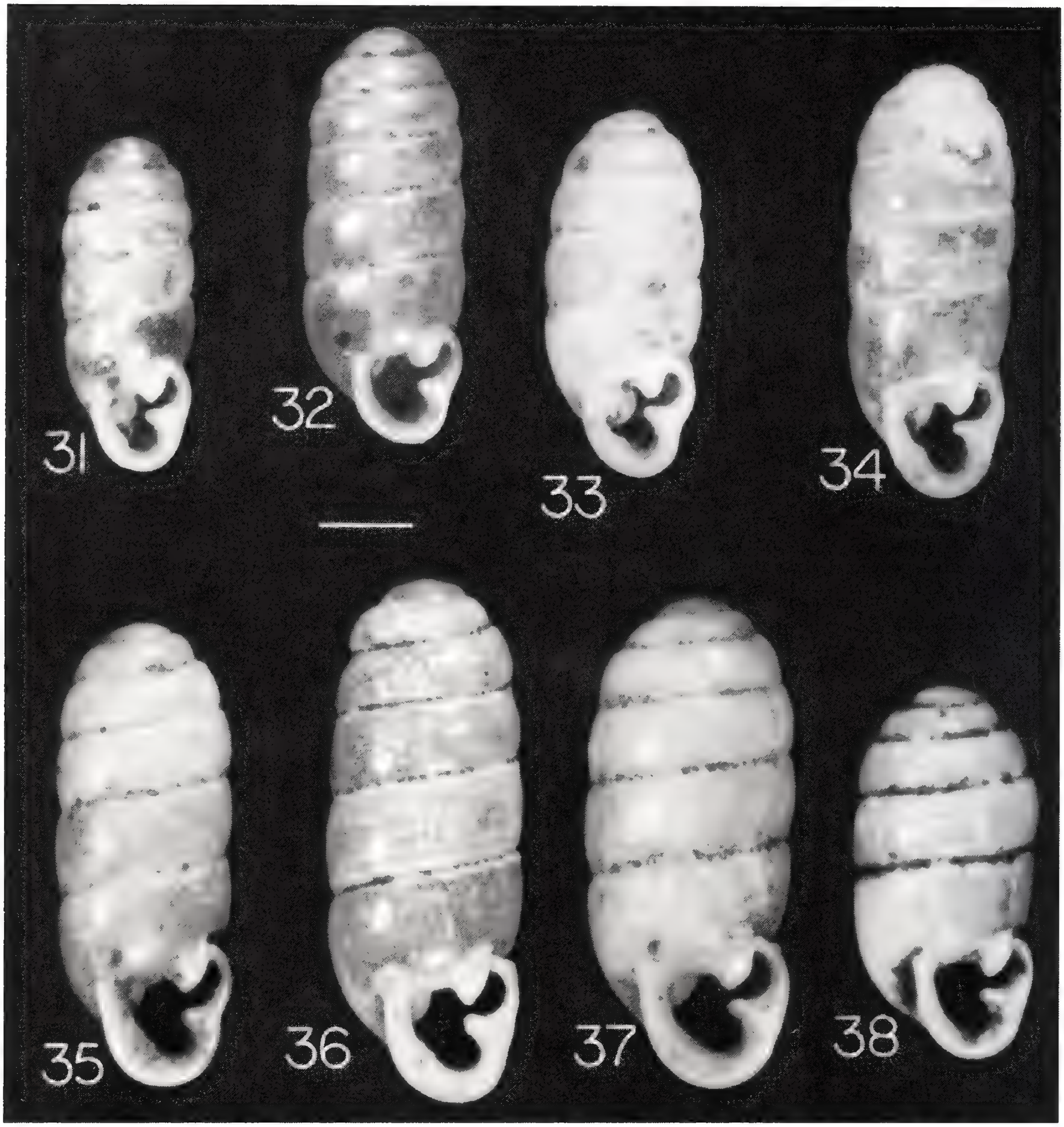
DIAGNOSIS. One of only two Madagascan species of *Gulella* with the apertural dentition limited to a small parietal tooth; the other is *G. rubinsterni. G. microdon* differs from *G. rubinsterni* in its much looser coiling (whorls/ln height 2.1 vs. 3.0).

DESCRIPTION (based on illustration in Fischer-Piette *et al.*, 1994). Height 13.0 mm, diameter 6.2 mm (H/D 2.1), whorls 5.5 (whorls/ln height 2.14). Apical angle 125°, barreling 0.0%. Sutural depth 1.1%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely, apparently, between upper and lower sutures. Peristome height 4.5 mm, width 4.8 mm (0.8 shell D; peristome H/W 0.9); apertural lip width 0.40 mm (0.09 peristome W). Apertural barriers consisting of a minute parietal tooth and a small columellar recessed baffle.

Gulella rubinsterni Fischer-Piette, Blanc,
Blanc and Salvat, 1994
Fischer-Piette *et al.* (1994): fig. 53 (holotype)

DIAGNOSIS. One of only two Madagascan species of *Gulella* with the apertural dentition limited to a small parietal tooth; the other is *G. microdon. G. rubinsterni* differs from *G. microdon* in its much tighter coiling (whorls/ln height 3.0 vs. 2.1).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 15.0 mm, diameter 7.4 mm (H/D 2.0), whorls 8.0 (whorls/ln height 2.95). Apical angle 110°, barreling -2.5%. Sutural depth 6.1%. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and



Figs. 31-38. Fig. 31. *Gulella ankaranensis* Fischer-Piette, Blanc, Blanc and Salvat, 1994, specimen, Ankarana Reserve. Fig. 32. *G. fischerpiettei s.s.* sp. nov. holotype, Ankarana Reserve. Fig. 33. *G. fischerpiettei enigma* subsp. nov. holotype, Ankarana Reserve. Fig. 34. *G. satisfacta charlesblanci* subsp. nov. holotype, Ankarana Reserve. Fig. 35. *G. satisfacta vitsia* subsp. nov. holotype, Ankarana Reserve. Figs. 36-38. *G. satisfacta satisfacta* Fischer-Piette, Blanc, Blanc and Salvat, 1994, specimens, Ankarana Reserve. Scale bar 1 mm.

lower sutures. Peristome height 5.7 mm, width 4.8 mm (0.7 shell D; peristome H/W 1.2); apertural lip width 0.80 mm (0.16 peristome W). Apertural barriers consisting of a small parietal tooth and a small columellar recessed baffle. Umbilicus imperforate.

Gulella nifikelia sp. nov.

Fig. 2

DIAGNOSIS. *G. nifikelia* sp. nov. is somewhat similar to the South African *G. perspicuaeformis* (Sturany, 1898) but is much more loosely coiled. Of Madagascan *Gulella* with apertural dentition restricted to parietal and palatal teeth, *G. nifikelia* sp. nov. is unique in its combination of (a) parietal and palatal teeth minute and approximately equal in size, (b) shell height less than 4.5 mm (whorls/ln height 4.5), and (c) moderately strong rib sculpturing. Other species have parietal and palatal teeth small to large and generally unequal in size, or if small and approximately equal then shell height is greater than 6.5 mm (whorls/ln height 3.4) and rib sculpture is very weak to absent.

HOLOTYPE. Station 423 (UF 274964, 1 ad): 23°00'S, 47°44'E: Madagascar: Manombo Reserve, 50 m: rainforest. 21-Apr-95.

DESCRIPTION OF HOLOTYPE. Height 4.0 mm, diameter 1.8 mm (H/D 2.2), whorls 6.2 (whorls/ln height 4.47). Apical angle 75°, barreling 1.1%. Sutural depth 4.4%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.88 mm, embryonic sculpture smooth, with a trace of growth lines or riblets. Peristome height 1.2 mm, width 1.3 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.22 mm (0.17 peristome W). Apertural barriers consisting of a small parietal tooth; a small palatal tooth (parietal-palatal embayment extremely wide); and a small columellar recessed baffle. Umbilicus a very narrow well.

ETYMOLOGY. For the small size of the apertural barriers (Malagasy "nify" = teeth, "kely" = little).

Gulella bouchardi Fischer-Piette, Blanc and Vukadinovic, 1974

Fischer-Piette *et al.* (1994): plate V fig. 1 (holotype)

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to parietal and palatal teeth, (b) shell sculpture smooth or nearly so (but with a crenulate suture), and (c) parietal tooth small and parieto-palatal embayment wide, *G. bouchardi* is unique in its very loose coiling (whorls/ln height about 3.1). It is most similar to *G. masoalae*, which has tighter coiling (whorls/ln height 3.3-3.4).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 7.0 mm, diameter 3.1 mm (H/D 2.2), whorls 6.0 (whorls/ln height 3.08). Apical angle 100°, barreling 0.0%. Sutural depth 9.7%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 2.2 mm, width 2.0 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.30 mm (0.15 peristome W). Apertural barriers consisting of a minute parietal tooth; a small to moderate, triangular palatal tooth (parietal-palatal embayment wide); and a small columellar recessed baffle. Umbilicus a crevice, apparently.

Gulella masoalae sp. nov.

Fig. 3

DIAGNOSIS. *G. masoalae* sp. nov. is somewhat similar to the Comoran *G. diodon* (Morelet, 1882) but is much more loosely coiled. Among Madagascan *Gulella* with (a) apertural dentition restricted to parietal and palatal teeth, (b) shell sculpture smooth or nearly so (but with a crenulate suture), and (c) parietal tooth small and parieto-palatal embayment wide, *G. masoalae* sp. nov. is unique in its coiling (whorls/ln height 3.28-3.35). It is most similar to *G. bouchardi*, which has looser coiling (whorls/ln height 3.1), and to the sometimes sympatric *G. antongilae* sp. nov., which has both tighter coiling (whorls/ln height 3.38-3.58) and a smaller initial whorl (diameter of first 1.5 whorls 1.05-1.13 mm vs. 1.25-1.35 mm in *G. masoalae* sp. nov.). *G. masoalae* sp. nov. is somewhat similar to *G. marojejyae* sp. nov. in size, coiling, and apertural dentition, but is larger in initial-whorl size (diameter of first 1.5 whorls 1.25-1.35 mm *vs.* 1.0-1.1 mm) and has smooth (*vs.* half-ribbed) sculpture.

HOLOTYPE. Station 311 (UF 274928, 1 ad): 15°33'S, 49°59'E: Madagascar: W Masoala Peninsula, 430 m: hardwood rainforest. 27-Sep-95.

DRY PARATYPES. Stations 294 (1 juv, specimen lost); 295 (2 juv, specimens lost); 297 (1 juv, specimen lost); 306 (UF 274929, 1 juv); 307 (ANSP 403446, 1 ad); 308 (1 juv, specimen lost); 309 (15 juv, specimens lost); 310 (1 juv, specimens lost); 311 (UF 274930, 1 juv; AMS C203598, 1 ad]); 313 (MNHN, 1 ad); 314 (UF 274931, 1 ad, 3 juv).

ALCOHOL PARATYPES. Stations 307 (UF 275129, 2 juv); 311 (UF 275130, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 7.8 mm, diameter 3.3 mm (H/D 2.4), whorls 6.9 (whorls/ln height 3.35). Apical angle 80°, barreling 0.0%. Sutural depth 7.5%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.25 mm, embryonic sculpture smooth. Peristome height 2.4 mm, width 2.2 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.23 mm (0.10 peristome W). Apertural barriers consisting of a small parietal tooth; a large, butte-shaped palatal tooth (parietal-palatal embayment wide); and a small columellar recessed baffle. Umbilicus imperforate.

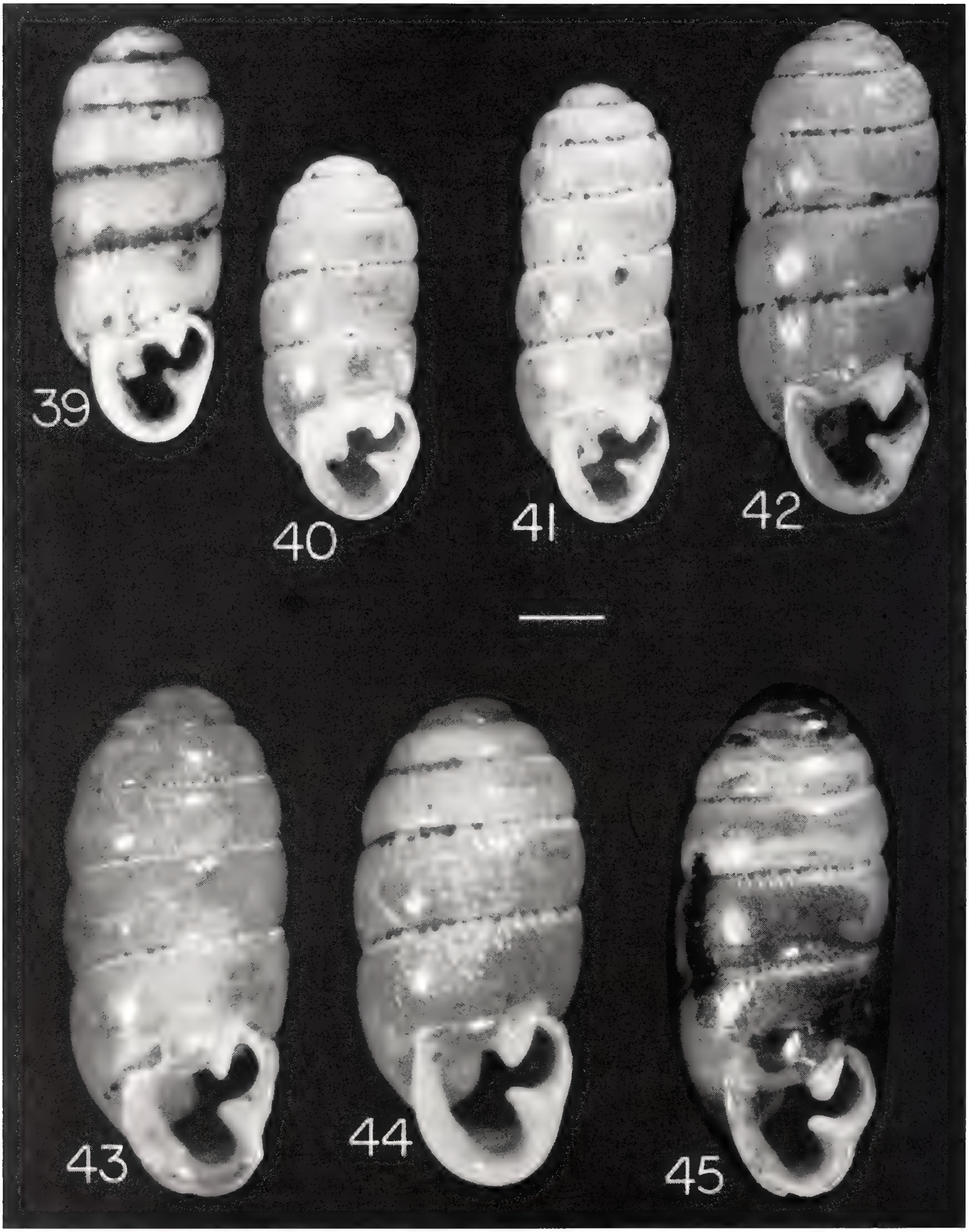
VARIATION. See Table 2.

ETYMOLOGY. For both Masoala National Park and the villagers of Masoala who helped collect.

Gulella antongilae sp. nov.

Figs. 4, 5, 6

DIAGNOSIS. *G. antongilae* sp. nov. is somewhat similar to the Comoran *G. diodon* (Morelet, 1882) but is more loosely coiled and its palatal tooth is lower in position and generally broader and squarer. Among Madagascan *Gulella* with (a) apertural dentition restricted to parietal and palatal teeth, (b) shell sculpture smooth or nearly so (but with a crenulate suture), and (c) parietal tooth small and parieto-palatal embayment wide, *G. antongilae* sp. nov. is unique in its tight coiling (whorls/ln height 3.38-3.58). It is most similar to the sometimes sympatric *G. masoalae* sp. nov., which differs in both its looser coiling (whorls/ln height 3.28-3.35) and its larger initial whorl (diameter of first 1.5



Figs. 39-45. Figs. 39, 40. *Gulella mahia* sp. nov.: Fig. 39 holotype, southern Cap d'Ambre; Fig. 40 paratype, type locality. Fig. 41. *G. ranomasina* sp. nov. holotype, northern Cap d'Ambre. Fig. 42. *G. jaominai* sp. nov. holotype, southern Cap d'Ambre. Fig. 43. *G. ambrensis s.s.* sp. nov. holotype, Montagne d'Ambre National Park. Fig. 44. *G. ambrensis andavakoerae* subsp. nov. holotype, Andavakoera massif. Fig. 45. *G. ambrensis rakotomalalai* sp. nov. holotype, Analamera Reserve. Scale bar 1 mm.

whorls 1.25-1.35 mm vs. 1.05-1.13 mm in *G. antongilae* sp. nov.).

HOLOTYPE. Station 300 (UF 274776, 1 ad): 15°47'S, 50°03'E: Madagascar: W Masoala Peninsula, 350 m: hardwood rainforest. 20-Sep-95.

FIGURED PARATYPES. Stations 364 (UF 274777, 1 ad); 723 (UF 274782, 1 ad).

OTHER DRY PARATYPES. Stations 294 (UF 274784, 2 ad); 295 (UF 274779, 1 juv); 297 (MNHN, 1 ad, 1 juv); 303 (ANSP 403447, 1 ad); 310 (AMS C203587, 1 ad, 1 juv); 363 (UF 274780, 2 ad; ANSP 403445, 1 ad); 365 (AMS C203605, 1 ad); 366 (UF 274783, 1 ad, 1 juv); 372 (MNHN, 1 juv); 723 (UF 274782, 1 juv); 724 (UF 274778, 1 juv); 756 (UF 274785, 1 ad, 1 juv); 758 (UF 274781, 1 ad).

ALCOHOL PARATYPES. Stations 283 (UF 275074, 1 ad); 285 (UF 275069, 3 ad); 294 (UF 275078, 1 ad, 3 juv); 295 (UF 275072, 1 juv); 300 (UF 275071, 1 juv); 303 (UF 275076, 1 ad, 1 juv); 310 (UF 275073, 2 juv); 363 (UF 275077, 1 ad); 723 (UF 275070, 1 ad); 724 (UF 275075, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.9 mm, diameter 2.7 mm (H/D 2.2), whorls 6.2 (whorls/ln height 3.50). Apical angle 85°, barreling 3.5%. Sutural depth 7.0%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 1.10 mm, embryonic sculpture smooth, with faint traces of growth lines. Peristome height 1.6 mm, width 1.7 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.19 mm (0.11 peristome W). Apertural barriers consisting of a very small parietal tooth; a moderate, broad, somewhat rectangular palatal tooth (parietal-palatal embayment wide); and a small columellar recessed baffle. Umbilicus imperforate.

VARIATION. See Tables 2, 3, 4.

ETYMOLOGY. For the Baie d'Antongil.

Gulella andreana Fischer-Piette,
Blanc and Vukadinovic, 1974
Fischer-Piette *et al.* (1994): plate V, fig. 2 (holotype)
Fig. 7 (specimen)

DIAGNOSIS. Among Madagascan *Gulella*, there are two species with (a) shell cylindrical and smooth, without sutural crenulation; (b) a columellar recessed baffle that is only shallowly recessed and is nubbed or bifid like a tooth; and (c) other apertural barriers limited to a smallish, sometimes weakly bifid parietal tooth, and a smaller, rounded-nub- or peg-shaped palatal tooth, separated by a wide embayment: *G. andreana* and *G. beandreana* sp. nov. *G. andreana* has a smaller shell for the same number of whorls (whorls/ln height about 3.9 vs. about 3.6) and a smaller initial whorl (diameter of first 1.5 whorls 0.9 mm vs. 1.1) than *G. beandreana* sp. nov.

FIGURED SPECIMEN. Station 32 (UF 274763, 1 ad).

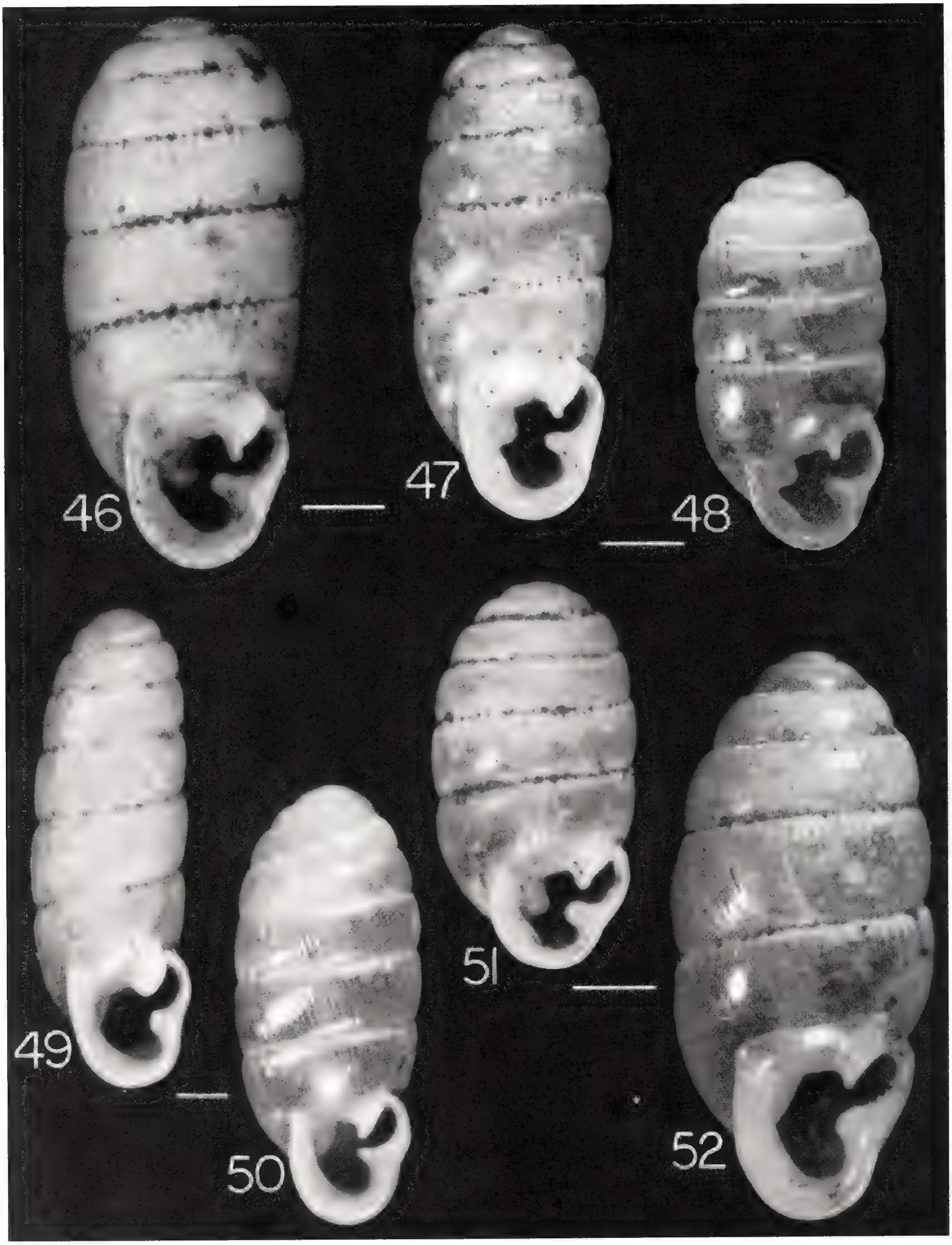
OTHER DRY VOUCHER SPECIMENS. Stations 32 (UF 274723, 4 ad, 4 juv); 42 (UF 274700, 1 ad); 43 (UF 274740, 2 ad, 6 juv); 49 (UF 274693, 1 ad); 55 (UF 274720, 7 ad, 5 juv); 56 (UF 274710, 4 ad, 2 juv); 58 (UF 274762, 4 ad, 3 juv); 61 (UF 274715, 73 ad, 91 juv; AMS C203566, 5 ad; ANSP 403448, 5 ad; MNHN, 5 ad); 62 (UF 274717, 94 ad, 50 juv); 63 (UF 274719, 91 ad, 87 juv); 64 (UF 274738, 1 ad, 1 juv); 65 (UF 274701, 10 ad, 1 juv); 68 (UF 274734, 18 ad, 17 juv); 69 (UF 274711, 6 ad, 2 juv); 70 (UF 274702, 5 ad, 3 juv); 71 (UF 274750, 4 ad); 72 (UF 274744, 1 ad, 3 juv); 81 (UF 274698, 1 juv); 82 (UF 274736, 4 ad, 7 juv); 83 (UF 274716, 52 ad, 88 juv); 84 (UF 274718, 24 ad, 29 juv); 168 (UF 274721, 3 ad); 218 (UF 274735, 5 ad, 9 juv); 221 (UF 274755, 8 ad); 222 (UF 274737, 3 ad, 2 juv); 233 (UF 274764, 2 ad, 1 juv); 234 (UF 274741, 3 ad, 1 juv); 238 (UF 274766, 10 ad, 2 juv); 239 (UF 274752, 1 ad); 241 (UF 274747, 1 ad); 252 (UF 274745, 3 ad, 1 juv); 254 (UF 274728, 5 ad, 17 juv); 255 (UF 274732, 4 ad, 8 juv); 400 (UF 274757, 3 ad, 2 juv); 401 (UF 274714, 1 ad, 1 juv); 403 (UF 274746, 1 ad, 1 juv); 404 (UF 274713, 1 ad, 2 juv); 408 (UF 274726, 15 ad, 2 juv); 411 (UF 274759, 3 ad, 2 juv); 439 (UF 274749, 11 ad, 4 juv); 440 (UF 274754, 6 ad, 1 juv); 441 (UF 274739, 2 ad, 4 juv); 442 (UF 274709, 12 ad, 5 juv); 443 (UF 274722, 8 ad, 3 juv); 444 (UF 274705, 4 ad, 1 juv); 445 (UF 274724, 8 ad, 1 juv); 447 (UF 274765, 1 ad, 1 juv); 448 (UF 274697, 3 ad, 2 juv); 449 (UF 274758, 3 ad); 450 (UF 274748, 5 ad); 451 (UF 274761, 6 ad, 3 juv); 458 (UF 274695, 3 ad); 459 (UF 274712, 10 ad); 460 (UF 274696, 3 ad, 2 juv); 461 (UF 274751, 10 ad, 4 juv); 462 (UF 274760, 2 ad, 2 juv); 463 (UF 274707, 1 ad, 1 juv); 466 (UF 274725, 1 ad, 2 juv); 483 (UF 274753, 2 ad, 2 juv); 484 (UF 274694, 1 juv); 489 (UF 274699, 3 ad, 4 juv); 494 (UF 274704, 7 ad, 19 juv); 558 (UF 274730, 4 ad, 4 juv); 565 (UF 274703, 2 ad, 1 juv); 570 (UF 274756, 7 ad, 14 juv); 572 (UF 274742, 1 ad); 803 (UF 274727, 1 ad, 2 juv); 810 (UF 274708, 1 ad); 813 (UF 274731, 7 ad, 10 juv); 815 (UF 274706, 4 ad); 816 (UF 274729, 3 juv); 818 (UF 274733, 5 ad, 5 juv).

ALCOHOL VOUCHER SPECIMENS. Stations 52 (UF 273694, 1 ad); 61 (UF 273710, 2 ad, 2 juv); 62 (UF 273696, 4 ad); 63 (UF 273704, 2 ad); 400 (UF 273709, 1 ad); 408 (UF 273711, 5 ad); 443 (UF 273697, 11 ad, 1 juv); 444 (UF 273701, 5 ad, 1 juv); 445 (UF 273703, 1 ad, 2 juv); 446 (UF 273702, 2 ad, 2 juv); 447 (UF 273708, 14 ad, 2 juv); 448 (UF 273700, 22 ad); 449 (UF 273695, 11 ad, 8 juv); 450 (UF 273690, 18 ad, 3 juv); 451 (UF 273698, 6 ad, 3 juv); 458 (UF 273692, 2 ad); 459 (UF 273693, 5 ad); 460 (UF 273713, 6 ad, 1 juv); 461 (UF 273705, 8 ad, 4 juv); 462 (UF 273706, 15 ad, 7 juv); 463 (UF 273714, 12 ad, 2 juv); 464 (UF 273707, 9 ad, 11 juv); 465 (UF uncatalogued, 5 ad, 3 juv, possibly lost); 466 (UF 273712, 7 ad, 6 juv); 565 (UF 273699, 1 juv).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 6.5 mm, diameter 1.9 mm (H/D 3.5), whorls 7.0 (whorls/ln height 3.74). Apical angle 90°, barreling -8.3%. Sutural depth 5.4%, sutural crenulation none. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 1.7 mm, width 1.6 mm (0.8 shell D; peristome H/W 1.1); apertural lip width 0.20 mm (0.08 peristome W). Apertural barriers consisting of a moderate parietal tooth; a small, peg-triangular palatal tooth (parietal-palatal embayment wide); and a small, nubbed, shallowly recessed columellar recessed baffle.

Gulella beandreana sp. nov.
Figs. 8, 9

DIAGNOSIS. Among Madagascan *Gulella*, there are two species with (a) shell cylindrical and smooth, without sutural crenulation; (b) a columellar recessed baffle that is only shallowly recessed and is nubbed or bifid like a tooth; and (c) other apertural dentition limited to a smallish, sometimes weakly bifid parietal tooth, and a smaller, rounded-nub- or peg-shaped palatal tooth, separated by a wide



Figs. 46-52. Fig. 46. *Gulella ambrensis capdambri* subsp. nov. holotype, northern Cap d'Ambre. Fig. 47. *G. ambrensis orangea* subsp. nov. holotype, Forêt d'Orange, Cap Mine. Fig. 48. *G. capmini* sp. nov. paratype, Cap Mine. Fig. 49. *G. bemarahae* sp. nov. holotype, Bemaraha Reserve. Fig. 50. *G. nakamaroa* sp. nov. holotype, Ankarana Reserve. Fig. 51. *G. capmini* sp. nov. holotype, Cap Mine. Fig. 52. *G. marojejyae* sp. nov. holotype, Marojejy Reserve. All scale bars 1 mm.

embayment: *G. beandreana* sp. nov. and *G. andreana. G. beandreana* sp. nov. is a rainforest species, and has a larger shell for the same number of whorls (whorls/ln height about 3.6 vs. about 3.9) and a larger initial whorl (diameter of first 1.5 whorls 1.1 mm vs. 0.9) than *G. andreana*, which is primarily a deciduous-forest species.

HOLOTYPE. Station 434 (UF 274786, 1 ad): 23°00'S, 47°44'E: Madagascar: Manombo Reserve, 50 m: rainforest. 23-Mar-96.

FIGURED PARATYPE. Station 712 (UF 274788, 1 ad).

OTHER DRY PARATYPES. Stations 677 (UF 274792, 2 ad, 1 juv); 679 (UF 274794, 8 ad, 2 juv); 680 (UF 274793, 10 ad; AMS C203568, 1 ad; ANSP 403449, 1 ad; MNHN, 1 ad); 712 (UF 274789, 3 ad, 1 juv); 715 (UF 274795, 3 ad, 1 juv); 716 (UF 274790, 1 ad); 717 (UF 274791, 4 ad, 2 juv).; 1402 (UF 274787, 1 ad).

ALCOHOL PARATYPES. Stations 435 (UF 275080, 2 ad); 679 (UF 275079, 1 ad); 717 (UF 275081, 1 juv).

DESCRIPTION OF HOLOTYPE. Height 6.9 mm, diameter 2.4 mm (H/D 2.9), whorls 6.9 (whorls/ln height 3.56). Apical angle 105°, barreling -1.3%. Sutural depth 2.7%, sutural crenulation none. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.11 mm, embryonic sculpture smooth. Peristome height 2.0 mm, width 2.0 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.22 mm (0.11 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, nub-shaped palatal tooth (parietal-palatal embayment wide); and a small, nubbed, bifid, shallowly recessed columellar recessed baffle. Umbilicus imperforate.

VARIATION. Columellar recessed baffle sometimes undivided.

ETYMOLOGY. For its resemblance to a large (Malagasy "be") version of *Gulella andreana*.

Gulella constricta sp. nov.

Fig. 10

DIAGNOSIS. Unique in having its aperture constricted centrally into an hourglass shape, and, amongst Madagascan *Gulella* with apertural dentition restricted to a parietal and a palatal tooth, in having its parietal tooth deeply recessed.

HOLOTYPE. Station 527 (UF 274820, 1 ad): 13°59'S, 48°47'E: Madagascar: Tsaratanana Reserve, 1395 m: rainforest. 17-Jun-95.

DESCRIPTION OF HOLOTYPE. Height 4.4 mm, diameter 1.8 mm (H/D 2.5), whorls 6.4 (whorls/ln height 4.35). Apical angle 115°, barreling 2.3%. Sutural depth 9.1%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.74 mm, embryonic sculpture of sutural notches. Aperture and peristome with a unique hourglass shape. Peristome height 1.3 mm, width 1.0 mm (0.6 shell D; peristome H/W 1.2); apertural lip width 0.12 mm (0.12 peristome W). Apertural barriers consisting of a massive, deeply recessed parietal tooth; a moderate, low and wide palatal tooth (parietal-palatal embayment narrow); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For the constricted (Latin "constricta") aperture.

Gulella ambatovakiae sp. nov.

Fig. 12

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent or weak, and (c) rib sculpture weak to none, *G. ambatovakiae* sp. nov. is unique in both its bifid parietal tooth and its triangular aperture.

HOLOTYPE. Station 766 (UF 274658, 1 ad): 16°43'S, 49°23'E: Madagascar: Ambatovaky Reserve, 400 m: rainforest. 27-Nov-95.

DESCRIPTION OF HOLOTYPE (broken and missing apex). Height (estimated) 4.6 mm, diameter (estimated) 2.3 mm (H/D 2.0). Barreling 2.7%. Sutural depth 10.5%, sutural crenulation apparently weak (but nearly completely eroded away). In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 1.2 mm, width 1.4 mm (0.6 shell D; peristome H/W 0.8); apertural lip width 0.18 mm (0.12 peristome W). Apertural barriers consisting of a moderate, bifid parietal tooth; a large, pegtriangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus imperforate.

ETYMOLOGY. For Ambatovaky Reserve.

Gulella magnifica sp. nov.

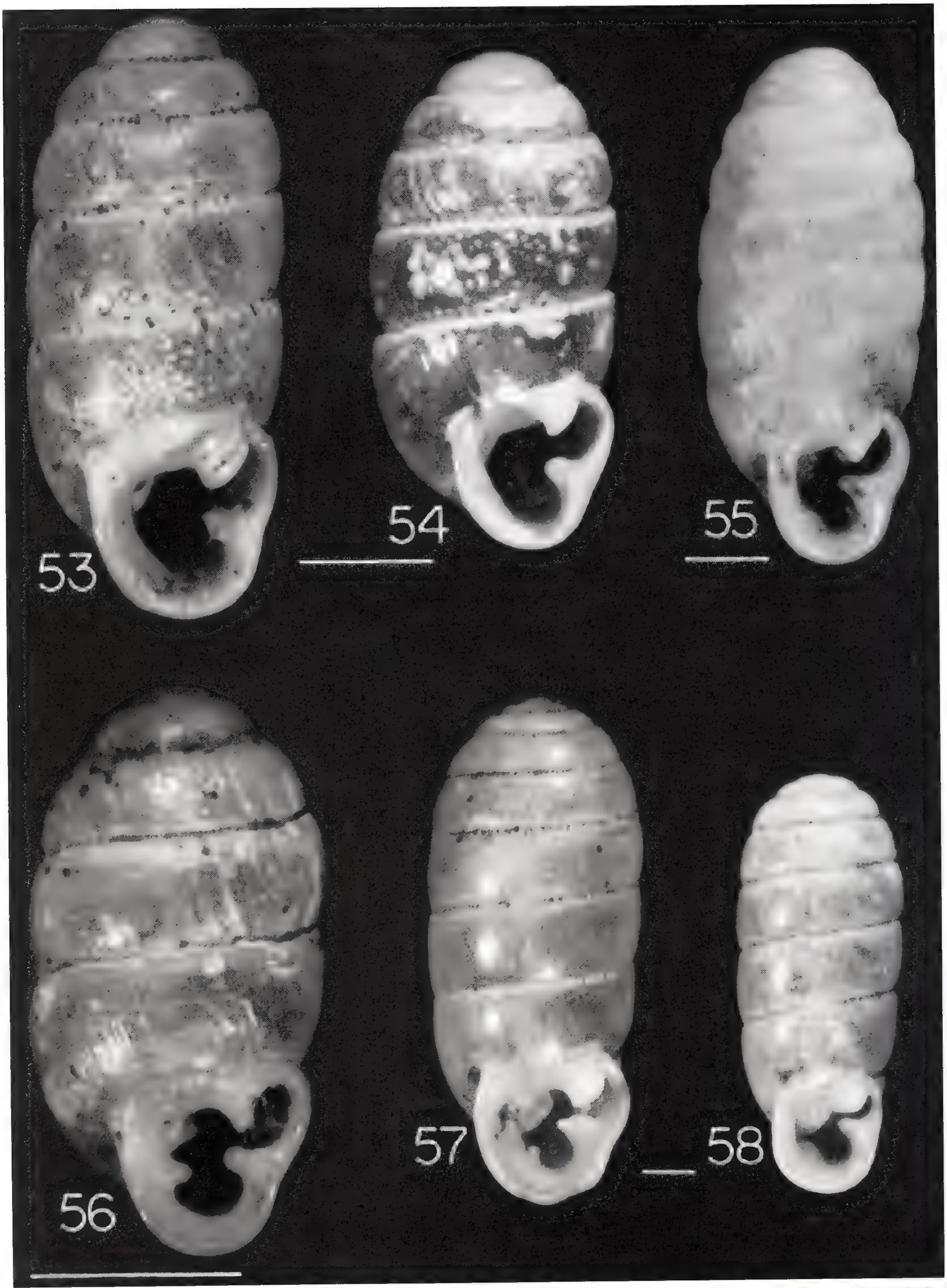
Fig. 11

DIAGNOSIS. *G. magnifica* sp. nov. is similar in shape and aperture to the Comoran *G. modioliformis* (Morelet, 1877) but has very much tighter coiling. Among Madagascan *Gulella* with (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella nonexistent or weak, and (c) rib sculpture weak to none, *G. magnifica* sp. nov. is unique in its great shell size (height greater than 11 mm) and large initial whorl (diameter of first 1.5 whorls 1.5 mm).

HOLOTYPE. Station 803 (UF 274879, 1 ad): 13°00'S, 49°01'E: Madagascar: Ankarana Reserve, 50 m. 8-Oct-94.

DRY PARATYPES. Stations 802 (AMS C203589, 1 ad; MNHN, 1 ad); 803 (UF 274880, 7 juv; AMS C203590, 8 juv); 807 (AMS C203591, 1 ad, 1 juv; ANSP 403450, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 12.6 mm, diameter 4.5 mm (H/D 2.8), whorls 9.3 (whorls/ln height 3.67). Apical angle 90°, barreling 4.4%. Sutural depth



Figs. 53-58. Fig. 53. *Gulella griffithsi* sp. nov. holotype, Bemaraha Reserve. Fig. 54. *G. tsara* sp. nov. holotype, Tsaratanana Reserve. Fig. 55. *G. microstriata* sp. nov. holotype, Ankarana Reserve. Fig. 56. *G. kelibea* sp. nov. holotype, Manombo Reserve. Fig. 57. *G. analamerae* sp. nov. holotype, Analamera Reserve. Fig. 58. *G. vohimarae* sp. nov. holotype, south of Vohimar. All scale bars 1 mm.

2.1%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.7, diameter of first 1.5 whorls 1.50 mm, embryonic sculpture of minute riblets, stronger above the suture, but faint throughout. Peristome height 3.3 mm, width 3.2 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.60 mm (0.19 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus an extremely minute crevice.

ETYMOLOGY. For the grand and splendid (Latin "magnifica") shell.

Gulella pseudandreana sp. nov.

Fig. 13

DIAGNOSIS. Among Madagascan *Gulella*, there are two species with (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent or weak, and (c) general rib sculpture weak but conspicuous: *G. pseudandreana* sp. nov. and *G. gallorum*. *G. pseudandreana* sp. nov. differs from *G. gallorum* in its smaller initial whorl (diameter of first 1.5 whorls 1.000-1.112 mm vs. 1.225-1.325 mm). *G. pseudandreana* differs from the similar *G. jaominai* sp. nov. in its weakly ribbed sculpture (*vs.* smooth sculpture) and its larger initial whorl (diameter of first 1.5 whorls 1.000-1.112 mm *vs.* 0.912-0.938 mm). In its size, coiling tightness, and columnar shape, *G. pseudandreana* sp. nov. bears superficial resemblance to *G. andreana*, from which it differs in its well recessed, broadly rounded columellar recessed baffle (*vs.* shallow, nubbed, and tooth-like), its sculpture of weak ribs (*vs.* smooth), and its larger initial whorl (diameter of first 1.5 whorls 1.0-1.1 *vs.* about 0.9).

HOLOTYPE. Station 245 (UF 274975, 1 ad): 19°08'S, 44°48'E: Madagascar: S Bemaraha Reserve, 70 m: dry forest. 14-Jun-95.

DRY PARATYPES. Stations 247 (UF 274978, 14 ad, 15 juv); 249 (UF274976, 4 ad, 7 juv; AMS C203607, 7 ad, 6 juv; ANSP 403451, 1 ad; MNHN, 1 ad); 250 (UF 274977, 3 ad, 5 juv); 251 (UF 274979, 1 ad, 3 juv).

DESCRIPTION OF HOLOTYPE. Height 6.3 mm, diameter 2.3 mm (H/D 2.8), whorls 7.2 (whorls/ln height 3.87). Apical angle 85°, barreling -1.4%. Sutural depth 4.2%, sutural crenulation moderate. In apertural view, penultimate and body whorls with weak rib sculpture that diminishes about three-fourths between upper and lower sutures. Embryonic whorls 2.2, diameter of first 1.5 whorls 1.11 mm, embryonic sculpture of faint growth lines or riblets. Peristome height 1.8 mm, width 1.8 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.25 mm (0.14 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, rounded-triangular palatal tooth (parietal-palatal embayment fairly wide); and a small columellar recessed baffle. Umbilicus a crevice.

VARIATION.	Station	#Sn	Wh/lnHt	D1st1.5Wh
	245	1	3.87	1.11
	247	2	3.78-3.94	1.00-1.05
	249	2	3.67-3.74	1.05-1.10

ETYMOLOGY. For its false (Greek "pseud-") resemblance to *Gulella andreana*.

Gulella gallorum Fischer-Piette, Blanc and Salvat, 1975

Fischer-Piette *et al.* (1994): plate IV, figs. 15-18 (holotype)

Fig. 14 (specimen)

DIAGNOSIS. Among Madagascan *Gulella*, there are two species with (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent or weak, and (c) general rib sculpture weak but conspicuous: *G. gallorum* and *G. pseudandreana* sp. nov., which also are similar in their cylindrical-to-columnar shapes. *G. gallorum* differs from *G. pseudandreana* sp. nov. in its larger initial whorl (diameter of first 1.5 whorls 1.225-1.325 mm *vs.* 1.000-1.112 mm). *G. gallorum* differs from the similar and sometimes sympatric *G. jaominai* sp. nov. in its weakly ribbed sculpture (*vs.* smooth sculpture), its looser coiling (whorls/ln height 3.71-3.90 *vs.* 3.90-3.98), and, especially, its much larger initial whorl (diameter of first 1.5 whorls 1.225-1.325 mm vs. 0.912-0.938 mm). *G. gallorum* differs from the similar *G. boucheti* (both of which occur on Montagne des Français: Fischer-Piette *et al.*, 1994) in its distinctly cylindrical (*vs.* barreled) shape and seemingly in its smaller initial whorl (diameter of first 1.5 whorls 1.22-1.32 mm *vs.* 1.35-1.36 mm).

FIGURED SPECIMEN. Station 401 (UF 274831, 1 ad).

OTHER DRY VOUCHER SPECIMENS. Stations 401 (UF 274832, 68 ad, 46 juv; AMS C203584, 3 ad; ANSP 403452, 3 ad; MNHN, 3 ad); 405 (UF 274833, 4 ad, 5 juv).

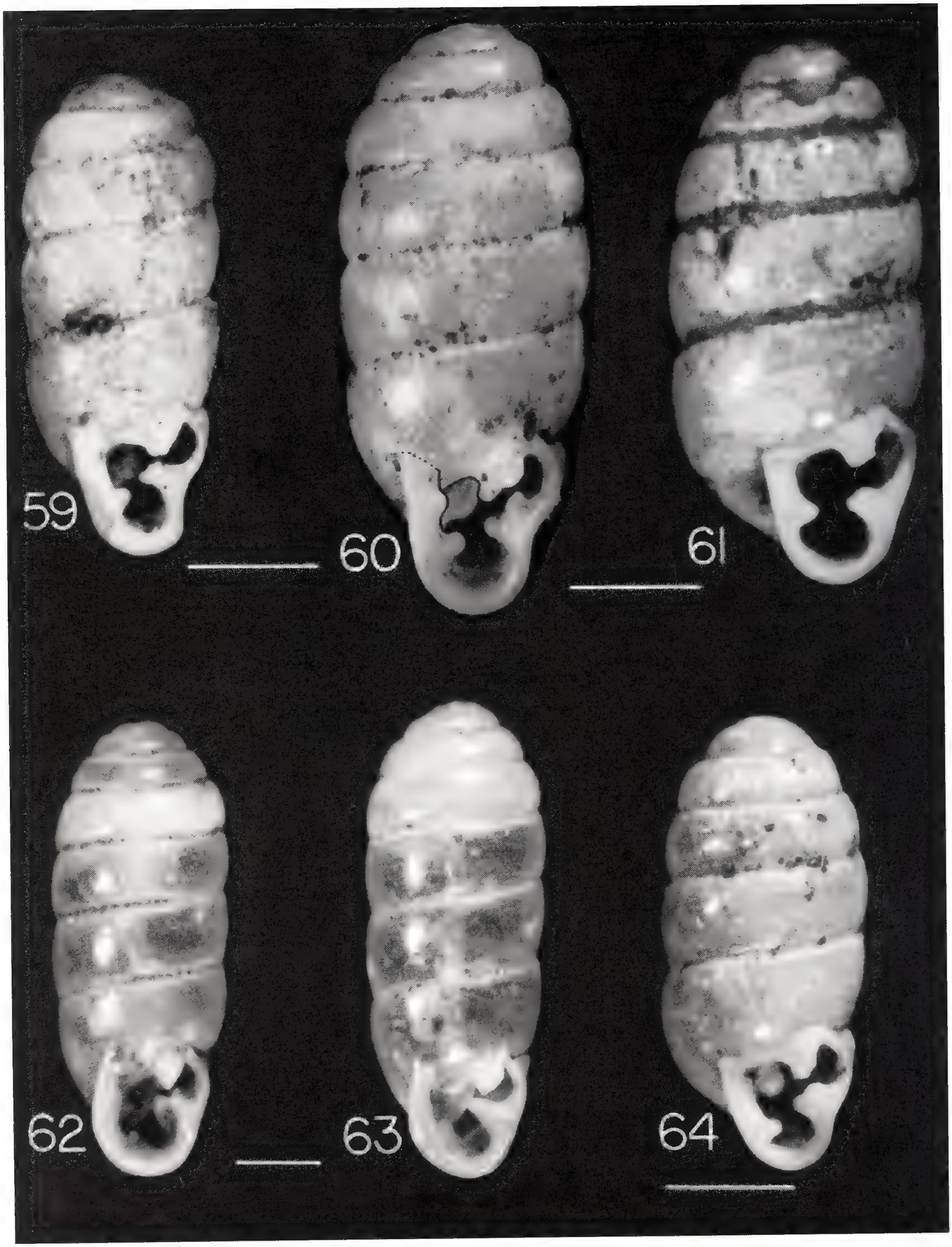
DESCRIPTION OF HOLOTYPE (from illustration in Fischer-Piette *et al.*, 1994). Height 9.2 mm, diameter 2.8 mm (H/D 3.2), whorls 8.3 (whorls/ln height 3.74). Apical angle 75°, barreling 0.0%. Sutural depth 8.0%, sutural crenulation moderate. In apertural view, penultimate and body whorls with weak rib sculpture that does not diminish between upper and lower sutures. Peristome height 2.3 mm, width 2.2 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.20 mm (0.07 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate to large, squared palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle.

VARIATION. See Table 2.

Gulella rakotoarisoni sp. nov.

Fig. 15

DIAGNOSIS. Among Madagascan *Gulella* species with (a) apertural dentition restricted to a parietal tooth and a



Figs. 59-64. Fig. 59. *Gulella tendronia* sp. nov. holotype, Analamera Reserve. Fig. 60. *G. celestinae* sp. nov. holotype, Namoroka Reserve. Fig. 61. *G. nosybei* sp. nov. holotype, Lokobe Reserve, Nosy Be. Fig. 62. *G. bemoka* sp. nov. holotype, northern Cap d'Ambre. Fig. 63. *G. vavakelia* sp. nov. holotype, Analamera Reserve. Fig. 64. *G. mitsikia* sp. nov. holotype, Ankarana Reserve. All scale bars 1 mm.

palatal tooth, (b) baso-columellar lamella non-existent or weak, (c) rib sculpture absent or weak and inconspicuous, (d) height less than 9 mm and diameter of first 1.5 whorls less than 1.4 mm, and (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, *G. rakotoarisoni* sp. nov. is unique for its very large parietal and palatal teeth and its conspicuous columellar recessed baffle. *G. rakotoarisoni* sp. nov. bears some resemblance to *G. zanaharyi* sp. nov., but differs in its much smaller columellar recessed baffle and its lack of either a strong baso-columellar lamella or a baso-columellar tooth.

HOLOTYPE. Station 580 (UF 274980, 1 ad): 12°58'S, 49°05'E: Madagascar: Ankarana Reserve, 95 m: dry deciduous forest. 26-Aug-95.

DRY PARATYPES. Stations 570 (UF 274981, 1 ad, 1 juv); 572 (ANSP 403453, 1 ad, 1 juv); 580 (AMS C203608, 1 ad, 1 juv); 581 (MNHN, 1 ad, 3 juv).

DESCRIPTION OF HOLOTYPE. Height 4.4 mm, diameter 1.9 mm (H/D 2.4), whorls 6.1 (whorls/ln height 4.09). Apical angle 95°, barreling 1.1%. Sutural depth 4.3%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.93 mm, embryonic sculpture smooth. Peristome height 1.4 mm, width 1.4 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.29 mm (0.21 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus imperforate, apparently.

ETYMOLOGY. For Jean Rakotoarison, Projet Parc National de Ranomafana, trusty and hard-working associate in both field and lab, who helped collect this species.

Gulella boucheti Fischer-Piette, Blanc, Blanc and Salvat, 1994

Fischer-Piette *et al.* (1994): fig. 55 (holotype)

Figs. 16, 17 (specimens)

DIAGNOSIS. Two species of Madagascan *Gulella* share (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent or weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible in apertural view, (g) palatal tooth low, broad, and squarish, (h) sutures shallowly impressed, (i) embryonic whorls 1.6 to 1.7, and (j) diameter of first 1.5 whorls 1.2 to 1.4 mm: *G. boucheti* and *G. petitboucheti* sp. nov. *G. boucheti* is distinctly more loosely coiled than *G. petitboucheti* sp. nov. (whorls/ln height about 3.6-3.8 *vs.* about 4.3) and has a larger initial whorl (diameter of first 1.5 whorls about 1.4 mm *vs.* about 1.2 mm). *G. boucheti* differs from the similar *G. gallorum* (both of which occur on Montagne des Français: Fischer-Piette e*t al.*, 1994) in its barreled (*vs.* cylindrical) shape and seemingly in its larger initial whorl (diameter of first 1.5 whorls 1.35-1.36 mm *vs.* 1.22-1.32 mm). *G. boucheti* resembles *G. lohabea* sp. nov. but lacks its baso-columellar lamella and has a larger initial whorl (diameter of first 1.5 whorls 1.35-1.36 mm *vs.* 1.28 mm).

FIGURED SPECIMENS. Stations 218 (UF 274810, 1 ad); 222 (UF 274809, 1 ad).

OTHER DRY VOUCHER SPECIMENS. Stations 217 (UF 274813, 9 ad, 2 juv); 218 (UF 274814, 6 ad, 4 juv); 221 (UF 274812, 320 ad, 30 juv; AMS C203573, 5 ad; ANSP 403454, 5 ad; MNHN, 5 ad); 222 (UF 274811, 8 ad).

ALCOHOL VOUCHER SPECIMENS. Stations 221 (UF 275083, 29 ad, 6 juv); 222 (UF 275082, 1 juv).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994, which seems to be a neoadult with aperture not fully developed). Height 6.4 mm, diameter 2.9 mm (H/D 2.2), whorls 7.0 (whorls/ln height 3.77). Apical angle 85°, barreling 12.9%. Sutural depth 3.2%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 1.6 mm, width 1.8 mm (0.6 shell D; peristome H/W 0.9); apertural lip width 0.20 mm (0.08 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate to large, triangular palatal tooth (parietal-palatal embayment fairly wide); and a small columellar recessed baffle. Umbilicus a crevice.

VARIATION. See Tables 2, 3.

Gulella petitboucheti sp. nov.

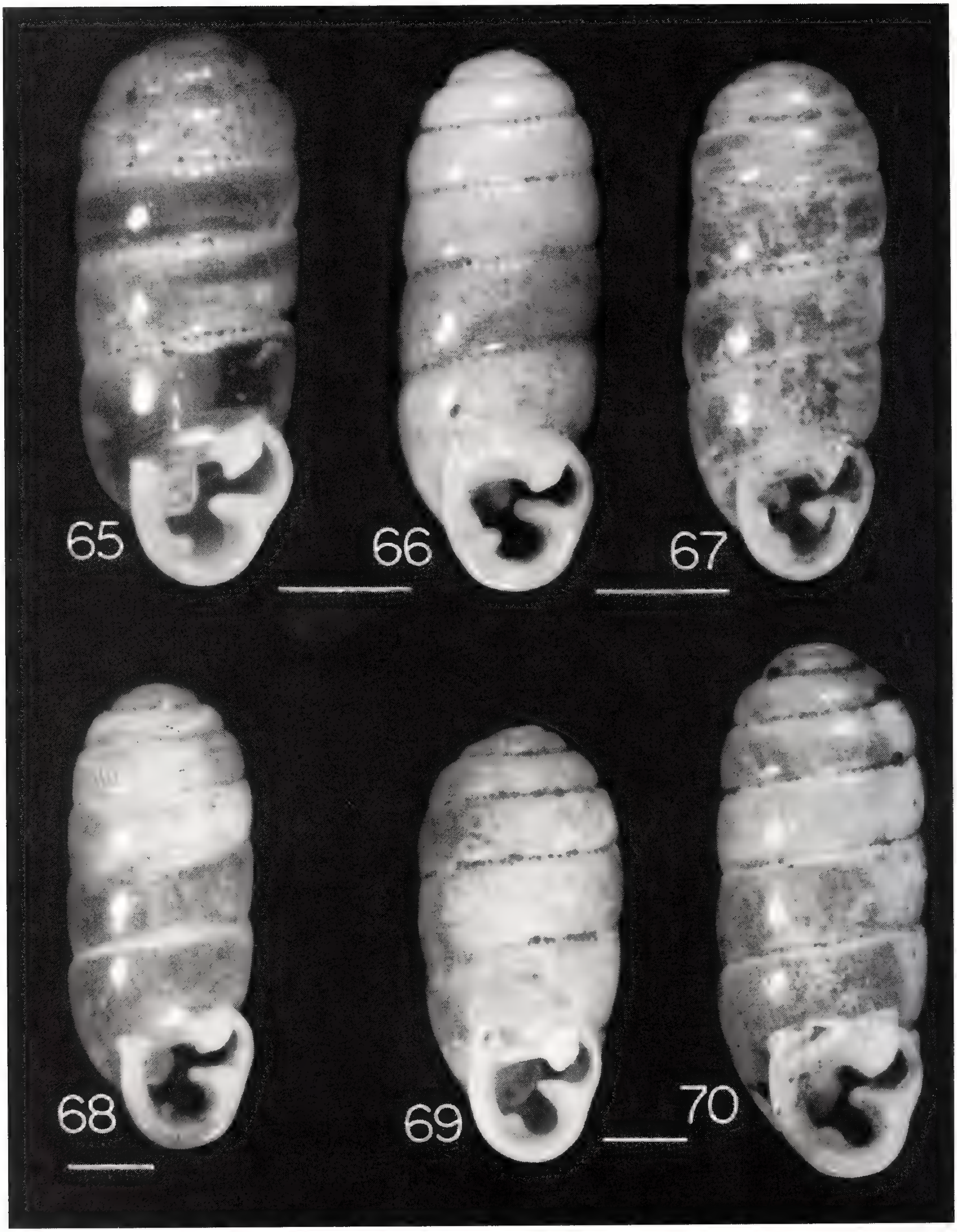
Fig. 18

DIAGNOSIS. There are only two species of Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella non-existent or weak, (c) general rib sculpture absent or weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth low, broad, and squarish, (h) sutures shallowly impressed, (i) embryonic whorls 1.6 to 1.7, and (j) diameter of first 1.5 whorls 1.2 to 1.4 mm: *G. petitboucheti* sp. nov. and *G. boucheti*. *G. petitboucheti* sp. nov. is distinctly more tightly coiled than *G. boucheti* (whorls/ln height about 4.3 *vs.* about 3.6-3.8) and has a smaller initial whorl (diameter of first 1.5 whorls about 1.2 mm *vs.* about 1.4 mm).

HOLOTYPE. Station 223 (UF 274972, 1 ad): 12°18'S, 49°20'E: Madagascar: Montagne des Français, 70 m: dry deciduous forest. 21-Jul-95.

DRY PARATYPES. Stations 222 (UF 274973, 4 ad); 223 (UF 274974, 1 ad, 3 juv; AMS C203606, 1 ad; ANSP 403455, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.5 mm, diam-



Figs. 65-70. Figs. 65-67. *Gulella bobaombiae* sp. nov.: Fig. 65 holotype, southern Cap d'Ambre; Fig. 66 paratype, Montagne des Français; Fig. 67 paratype, northern tip of Cap d'Ambre. Fig. 68. *G. ambanikelia* sp. nov. holotype, Ankarana Reserve. Figs. 69-70. *G. zanaharyi* sp. nov. paratypes: Fig. 69 northern Cap d'Ambre; Fig. 70 southern Cap d'Ambre. All scale bars 1 mm.

eter 2.4 mm (H/D 2.3), whorls 7.4 (whorls/ln height 4.34). Apical angle 95°, barreling 7.7%. Sutural depth 3.8%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.6, diameter of first 1.5 whorls 1.18 mm, embryonic sculpture smooth. Peristome height 1.7 mm, width 1.6 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.21 mm (0.13 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, very low, rounded-rectangular palatal tooth (parietal-palatal embayment fairly wide); and a small columellar recessed baffle. Umbilicus a crevice.

VARIATION. See Table 2.

ETYMOLOGY. For its resemblance to a miniature *Gulella boucheti*, with which this species is sympatric.

Gulella reeae Emberton and Pearce, 2000

Fig. 19

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent to weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth elevated, narrow, and triangular or pegged, (h) sutures moderately impressed, (i) embryonic whorls 1.8 to 2.2, and (j) diameter of first 1.5 whorls 0.8 to 1.0 mm, three species are distinguished from *G. fotobohitrae* sp. nov. and *G. razafyi* sp. nov. by their tighter coiling (whorls/ln height 4.4-4.7 *vs.* 4.0-4.3): *G. reeae, G. miaranoniae* sp. nov., and *G. bebokae* sp. nov. *G. reeae* differs from the latter two in its larger initial whorl (diameter of first 1.5 whorls about 0.95 mm *vs.* about 0.80-0.81 mm) and its weak (*vs.* strong) sutural crenulation.

DESCRIPTION OF HOLOTYPE (USNM 860807). Height 4.4 mm, diameter 1.8 mm (H/D 2.4), whorls 6.5 (whorls/ln height 4.36). Apical angle 75°, barreling 0.0%. Sutural depth 7.4%, sutural crenulation weak. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.94 mm, embryonic sculpture smooth, with a faint trace of growth lines or riblets. Peristome height 1.3 mm, width 1.3 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.27 mm (0.20 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, triangular palatal tooth (parietal-palatal embayment wide); and a small columellar recessed baffle. Umbilicus a crevice.

Gulella miaranoniae sp. nov.

Fig. 20

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent to weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth elevated, narrow, and triangular or pegged, (h) sutures moderately impressed, (i) embryonic whorls 1.8 to 2.2, and (j) diameter of first 1.5 whorls 0.8 to 1.0 mm, three species are distinguished from both *G. fotobohitrae* sp. nov. and *G. razafyi* sp. nov. by their tighter coiling (whorls/ln height 4.4-4.7 *vs.* 4.0-4.3): *G. miaranoniae* sp. nov., *G. reeae*, and *G. bebokae* sp. nov. *G. miaranoniae* differs from *G. reeae* in its smaller initial whorl (diameter of first 1.5 whorls about 0.80-0.81 mm *vs.* about 0.95 mm) and its strong (*vs.* weak) sutural crenulation. *G. miaranoniae* differs from *G. bebokae* in its looser coiling (whorls/ln height about 4.5 *vs.* about 4.7), proportionally smaller peristome (0.5 *vs.* 0.7 shell diameter), and rainforest (*vs.* semi-deciduous forest) habitat.

HOLOTYPE. Station 446 (UF 274932, 1 ad): 21°10'S, 47°33'E: Madagascar: Miaranony, E Ranomafana National Park, 630 m: rainforest. 28-Nov-95.

DRY PARATYPES. Stations 439 (UF 274933, 2 ad); 440 (AMS C203610, 1 ad); 441 (UF 274935, 1 ad, 2 juv); 443 (MNHN, 1 ad); 446 (ANSP 403456, 1 ad); 447 (UF 274936, 1 ad); 451 (UF 274935, 2 juv).

ALCOHOL PARATYPE. Station 443 (UF 275131, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.9 mm, diameter 1.8 mm (H/D 2.2), whorls 6.2 (whorls/ln height 4.52). Apical angle 95°, barreling 0.0%. Sutural depth 5.8%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.81 mm, embryonic sculpture smooth. Peristome height 0.9 mm, width 0.8 mm (0.5 shell D; peristome H/W 1.0); apertural lip width 0.22 mm (0.27 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, rounded-peg-shaped palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus minute.

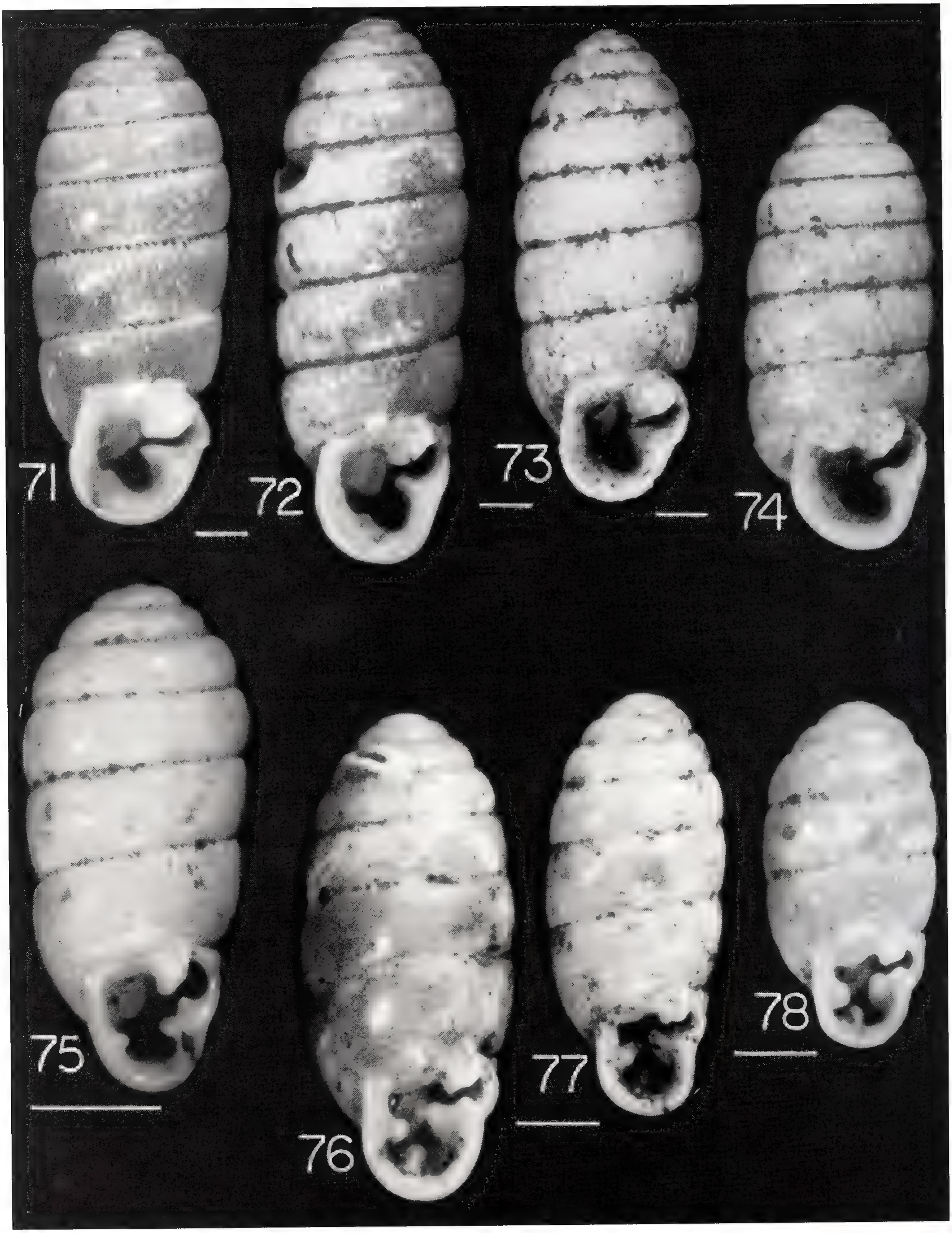
VARIATION.	Station	#Sn	Wh/lnHt	D1st1.5Wh
	439	1	4.54	0.80
	446	1	4.52	0.81
	447	1	4.48	0.81

ETYMOLOGY. For the forest and village of Miaranony, on the border of Ranomafana National Park.

Gulella bebokae sp. nov.

Fig. 21

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent to weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e)



Figs. 71-78. Figs. 71-74. *Gulella ambalaniranae* sp. nov. (to same size scale): Fig. 71 holotype, Mount Ambalanirana; Figs. 72-74 paratypes, near Mount Ambalanirana. Fig. 75. *G. namorokae* sp. nov. holotype, Namoroka Reserve. Figs. 76-78. *G. mihomehia* sp. nov. (to same size scale): Fig. 76 holotype, Ankarana Reserve; Fig. 77, 78 paratypes, Ankarana Reserve. All scale bars 1 mm.

shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth elevated, narrow, and triangular or pegged, (h) sutures moderately impressed, (i) embryonic whorls 1.8 to 2.2, and (j) diameter of first 1.5 whorls 0.8 to 1.0 mm, three species are distinguished from both *G. fotobohitrae* sp. nov. and *G. razafyi* sp. nov. by their tighter coiling (whorls/ln height 4.4-4.7 *vs.* 4.0-4.3): *G. bebokae* sp. nov., *G. reeae*, and *G. miaranoniae* sp. nov. *G. bebokae* sp. nov. differs from *G. reeae* in its smaller initial whorl (diameter of first 1.5 whorls about 0.80 mm *vs.* about 0.95 mm) and its strong (*vs.* weak) sutural crenulation. *G. bebokae* sp. nov. differs from *G. miaranoniae* sp. nov. in its tighter coiling (whorls/ln height about 4.7 *vs.* about 4.5), proportionally larger peristome (0.7 vs. 0.5 shell diameter), and semi-deciduous forest (*vs.* rainforest) habitat.

HOLOTYPE. Station 494 (UF 274796, 1 ad): 18°45'S, 44°45'E: Madagascar: N Bemaraha Reserve, 280 m: semi-deciduous forest. 29-Jun-96.

DRY PARATYPES. Station 494 (UF 274797, 1 ad, 1 juv; AMS C203569, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.7 mm, diameter 1.7 mm (H/D 2.2), whorls 6.1 (whorls/ln height 4.67). Apical angle 115°, barreling 4.5%. Sutural depth 6.8%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.80 mm, embryonic sculpture smooth. Peristome height 1.2 mm, width 1.3 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.16 mm (0.13 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For the Beboka River, Bemaraha Reserve.

Gulella fotobohitrae sp. nov.

Fig. 22

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent to weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth elevated, narrow, and triangular or pegged, (h) sutures moderately impressed, (i) embryonic whorls 1.8 to 2.2, and (j) diameter of first 1.5 whorls 0.8 to 1.0 mm, two species are distinguished from *G. reeae, G. miaranoniae* sp. nov., and *G. bebokae* sp. nov. by their looser coiling (whorls/ln height 4.0-4.3 *vs.* 4.4-4.7): *G. fotobohitrae* sp. nov. and *G. razafyi* sp. nov. *G. fotobohitrae* sp. nov. differs from *G. razafyi* sp. nov. in its looser coiling (whorls/ln height 4.0 *vs.* 4.2-4.3) and larger initial whorl (diameter of first 1.5 whorls 0.92-1.01 mm *vs.* 0.84 mm).

HOLOTYPE. Station 1389 (UF 274829, 1 ad): 21°21'S, 47°51'E: Madagascar: Fotobohitra, 350 m. 27-Sep-92.

DRY PARATYPES. Stations 1389 (AMS C203579, 1 ad; ANSP 403457, 1 ad); 1391 (ANSP 403458, 1 ad).

DESCRIPTION OF HOLOTYPE (an eroded shell). Height 5.8 mm, diameter 2.7 mm (H/D 2.2), whorls 7.0 (whorls/ln height 3.99). Apical angle 105°, barreling 3.5%. Sutural depth 4.9%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.01 mm, embryonic sculpture smooth. Peristome height 2.0 mm, width 1.7 mm (0.6 shell D; peristome H/W 1.2); apertural lip width 0.34 mm (0.21 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus a very narrow crevice.

VARIATION.	Station	#Sn	Wh/lnHt	D1st1.5Wh
	1389	1ad,1juv	3.99	0.98-1.01
	1391	1	4.06	0.92

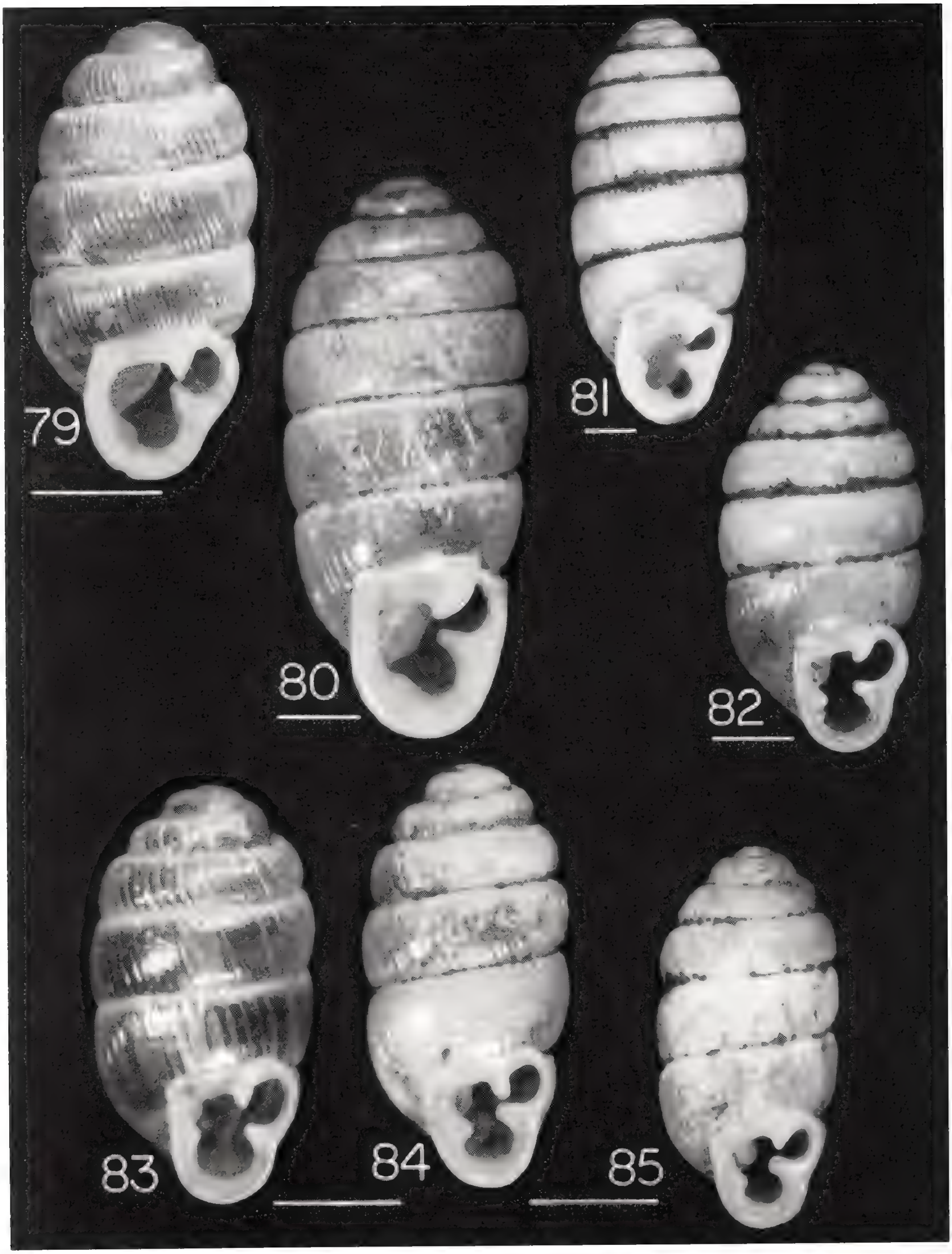
ETYMOLOGY. For Fotobohitra, the type locality.

Gulella razafyi sp. nov.

Fig. 23

DIAGNOSIS. *G. razafyi* sp. nov. is somewhat similar to the Comoran *G. oryza* (Morelet, 1882) but is much more loosely coiled. Among Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent to weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth elevated, narrow, and triangular or pegged, (h) sutures moderately impressed, (i) embryonic whorls 1.8 to 2.2, and (j) diameter of first 1.5 whorls 0.8 to 1.0 mm, two species are distinguished from *G. reeae, G. miaranoniae* sp. nov., and *G. bebokae* sp. nov. by their looser coiling (whorls/ln height 4.0-4.3 *vs.* 4.4-4.7): *G. razafyi* sp. nov. and *G. fotobohitrae* sp. nov. *G. razafyi* sp. nov. differs from *G. fotobohitrae* sp. nov. in its tighter coiling (whorls/ln height 4.2-4.3 *vs.* 4.0) and smaller initial whorl (diameter of first 1.5 whorls 0.84 mm *vs.* 0.92-1.01 mm).

HOLOTYPE. Station 1549 (UF 274986, 1 ad): 17°54'S, 49°12'E: Madagascar: Betampona Reserve, 400 m. 16-May-93.



Figs. 79-85. Fig. 79. *Gulella manomboae* sp. nov. holotype, Manombo Reserve. Fig. 80. *G. michellae* sp. nov. holotype, Marojejy Reserve. Fig. 81. *G. mahagaga* sp. nov. holotype, Tsaratanana Reserve. Fig. 82. *G. hafa* sp. nov. holotype, Marojejy Reserve. Figs. 83-84. *G. benjamini s.s.* Emberton and Pearce, 2000 (to same size scale): Fig. 83 holotype, northwest of Fort Dauphin; Fig. 85 specimen, Pic Saint Louis, near Fort Dauphin. Fig 84. *G. benjamini saintelucensis* subsp. nov. (note tight coiling) holotype, Forêt Sainte Luce, north of Fort Dauphin. All scale bars 1 mm.

DESCRIPTION OF HOLOTYPE. Height 4.3 mm, diameter 2.0 mm (H/D 2.2), whorls 6.3 (whorls/ln height 4.28). Apical angle 85°, barreling 0.0%. Sutural depth 5.6%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.2, diameter of first 1.5 whorls 0.84 mm, embryonic sculpture smooth, with a very faint trace of growth wrinkles. Peristome height 1.5 mm, width 1.3 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.28 mm (0.21 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus an extremely minute crevice.

ETYMOLOGY. For Razafy of Betampona Reserve, the collector.

Gulella josephinae sp. nov.

Fig. 24

DIAGNOSIS. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, and (c) rib sculpture strong to moderate, only two species have shell height generally greater than 9 mm due to loose coiling (whorls/ln height 3.2-3.4): *G. josephinae* sp. nov. and *G. soulaiana. G. josephinae* sp. nov. differs from *G. soulaiana* in its looser coiling (whorls/ln height about 3.2 *vs.* about 3.4), the flattened (*vs.* rounded) peripheries of its middle whorls, and its dry-deciduous (*vs.* rainforest) habitat.

HOLOTYPE. Station 61 (UF 274852, 1 ad): 16°23'S, 45°18'E: Madagascar: Namoroka Reserve, 105 m: dry deciduous forest. 25-May-95.

DRY PARATYPES. Stations 61 (UF 274858, 32 ad, 27 juv); 62 (UF 274859, 7 ad, 6 juv); 67 (UF 274860, 5 ad, 1 juv); 68 (UF 274861, 16 ad, 6 juv); 69 (UF 274854, 62 ad, 67 juv; AMS C203585, 3 ad; ANSP 403459, 3 ad; MNHN, 3 ad); 70 (UF 274855, 55 ad, 57 juv); 71 (UF 274856, 1 ad); 72 (UF 274857, 2 ad, 3 juv); 73 (UF 274862, 10 ad, 11 juv); 74 (UF 274853, 60 ad, 46 juv).

ALCOHOL PARATYPES. Stations 61 (UF 275095, 1 ad); 63 (UF 275093, 1 juv); 68 (UF 275098, 1 ad); 69 (UF 275094, 2 ad, 1 juv); 70 (UF 275096, 1 juv); 73 (UF 275092, 1 ad); 74 (UF 275097, 1 juv).

DESCRIPTION OF HOLOTYPE. Height 9.8 mm, diameter 3.7 mm (H/D 2.6), whorls 7.3 (whorls/ln height 3.20). Apical angle 95°, barreling 4.1%. Sutural depth 4.0%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.6, diameter of first 1.5 whorls 1.68 mm, embryonic sculpture smooth, with traces of growth lines. Peristome height 2.8 mm, width 2.8 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.63 mm (0.23 peristome W). Apertural barriers consisting of a large parietal tooth; a small, rounded palatal tooth that is buttressed below (parietal-palatal embayment somewhat narrow); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For Josephine Djaohasara Emberton, wife of the author.

Gulella soulaiana Fischer-Piette in Fischer-Piette, Cauquoin and Testud, 1973

Fischer-Piette *et al.* (1994): plate IV, fig. 19 (holotype)

DIAGNOSIS. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, and (c) rib sculpture strong to moderate, only two species have shell height generally greater than 9 mm due to loose coiling (whorls/ln height 3.2-3.4): *G. soulaiana* and *G. josephinae* sp. nov. *G. soulaiana* differs from *G. josephinae* sp. nov. in its tighter coiling (whorls/ln height about 3.4 *vs.* about 3.2), the rounded (*vs.* flattened) peripheries of its middle whorls, and its rainforest (*vs.* deciduous-forest) habitat.

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 10.5 mm, diameter 4.4 mm (H/D 2.4), whorls 8.0 (whorls/ln height 3.40). Apical angle 90°, barreling 5.6%. Sutural depth 5.6%. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Peristome height 3.4 mm, width 2.9 mm (0.7 shell D; peristome H/W 1.2); apertural lip width 0.80 mm (0.28 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment fairly wide); and a small columellar recessed baffle. Umbilicus "a miniscule perforation."

Gulella rugosa sp. nov.

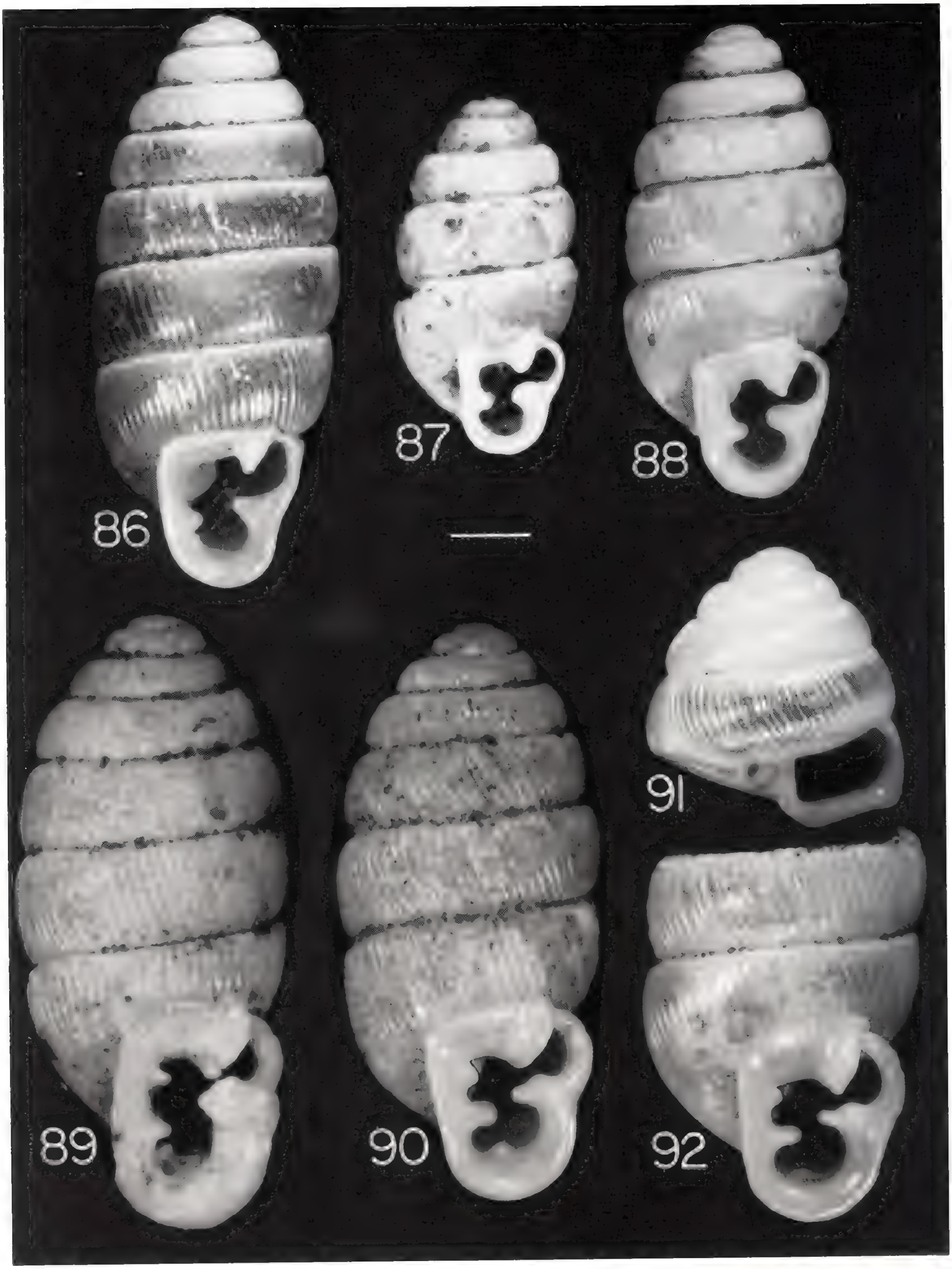
Fig. 25

DIAGNOSIS. *G. rugosa* sp. nov. is somewhat similar to the Comoran *G. spreta* (Morelet, 1883) but has a much blunter apex and is much more loosely coiled. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, and (c) shell height generally less than 7.5 mm due to tight coiling (whorls/ln height 3.7-4.4), only two species have very strong and high-standing rib sculpture: *G. rugosa* sp. nov. and *G. columna* sp. nov. *G. rugosa* sp. nov. differs from *G. columna* sp. nov. in its much looser coiling (whorls/ln height about 3.7 *vs.* about 4.1) and larger initial whorl (diameter of first 1.5 whorls about 1.0 mm *vs.* about 0.8 mm).

HOLOTYPE. Station 814 (UF 274987, 1 ad): 12°56'S, 49°07'E: Madagascar: Ankarana Reserve, 70 m. 11-Oct-94.

DRY PARATYPES. Station 814 (UF 274988, 1 juv; AMS C203611, 1 ad, 1 juv; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 7.2 mm, diameter 2.7 mm (H/D 2.7), whorls 7.4 (whorls/ln height 3.74). Apical angle 90°, barreling -2.4%. Sutural depth 2.4%,



Figs. 86-92. Figs. 86-88. *Gulella mahafinaratra* sp. nov.: Fig. 86 holotype, east of Marojejy Reserve; Figs. 87, 88 paratypes, Marojejy Reserve. Figs. 89-92. *G. hafahafa* sp. nov.: Fig. 89 holotype, south of Mananara; Fig. 90 paratype, Isle Sainte Marie; Figs. 91-92 paratypes, Betampona Reserve. Scale bar 1 mm.

sutural crenulation moderate. In apertural view, penultimate and body whorls with very strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls estimated at 1.7, diameter of first 1.5 whorls 1.00 mm, embryonic sculpture smooth, with a faint trace of growth lines or riblets. Peristome height 2.3 mm, width 2.1 mm (0.8 shell D; peristome H/W 1.1); apertural lip width 0.41 mm (0.19 peristome W). Apertural barriers consisting of a large parietal tooth; a moderate, broadly rounded palatal tooth (parietal-palatal embayment somewhat narrow); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For the coarsely ribbed, or wrinkled (Latin "rugosa") sculpture.

Gulella columna sp. nov.
Fig. 26

DIAGNOSIS. *G. columna* sp. nov. is somewhat similar to the Comoran *G. spreta* (Morelet, 1883) but is more loosely coiled and has a slenderer, more columnar shape. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, and (c) shell height generally less than 7.5 mm due to tight coiling (whorls/ln height 3.7-4.4), only two species have very strong and high-standing rib sculpture: *G. columna* sp. nov. and *G. rugosa* sp. nov. *G. columna* sp. nov. differs from *G. rugosa* sp. nov. in its much tighter coiling (whorls/ln height about 4.1 *vs.* about 3.7) and smaller initial whorl (diameter of first 1.5 whorls about 0.8 mm *vs.* about 1.0 mm).

HOLOTYPE. Station 807 (UF uncatalogued, 1 ad, possibly lost): 12°54'S, 49°06'E: Madagascar: Ankarana Reserve, 90 m. 10-Oct-94.

DRY PARATYPE. Station 807 (AMS C203576, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 6.3 mm, diameter 2.3 mm (H/D 2.8), whorls 7.6 (whorls/ln height 4.13). Apical angle 105°, barreling -1.4%. Sutural depth 12.0%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.6, diameter of first 1.5 whorls 0.84 mm, embryonic sculpture smooth. Peristome height 1.8 mm, width 1.7 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.28 mm (0.16 peristome W). Apertural barriers consisting of a large parietal tooth; a large, rounded palatal tooth (parietal-palatal embayment somewhat narrow); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For the shape and sculpture reminiscent of a Greek architectural column (Latin "columna").

Gulella pearcei sp. nov.
Fig. 27

DIAGNOSIS. *G. pearcei* sp. nov. is somewhat similar to the South African *G. rogersi* (Melvill and Ponsonby, 1898) in apertural morphology, size, and coiling tightness, but is slenderer and less columnar, with a sharper apex; its aperture is proportionally much smaller; and its palatal tooth is bifid instead of undivided. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, and (c) strong to moderate rib sculpture, *G. pearcei* sp. nov. is unique in having its palatal tooth high in position and notched opposite the parietal tooth.

HOLOTYPE. Station 222 (UF 274971, 1 ad): 12°19'S, 49°20'E: Madagascar: Montagne des Français, 230 m: dry deciduous forest, 21-Jul-95.

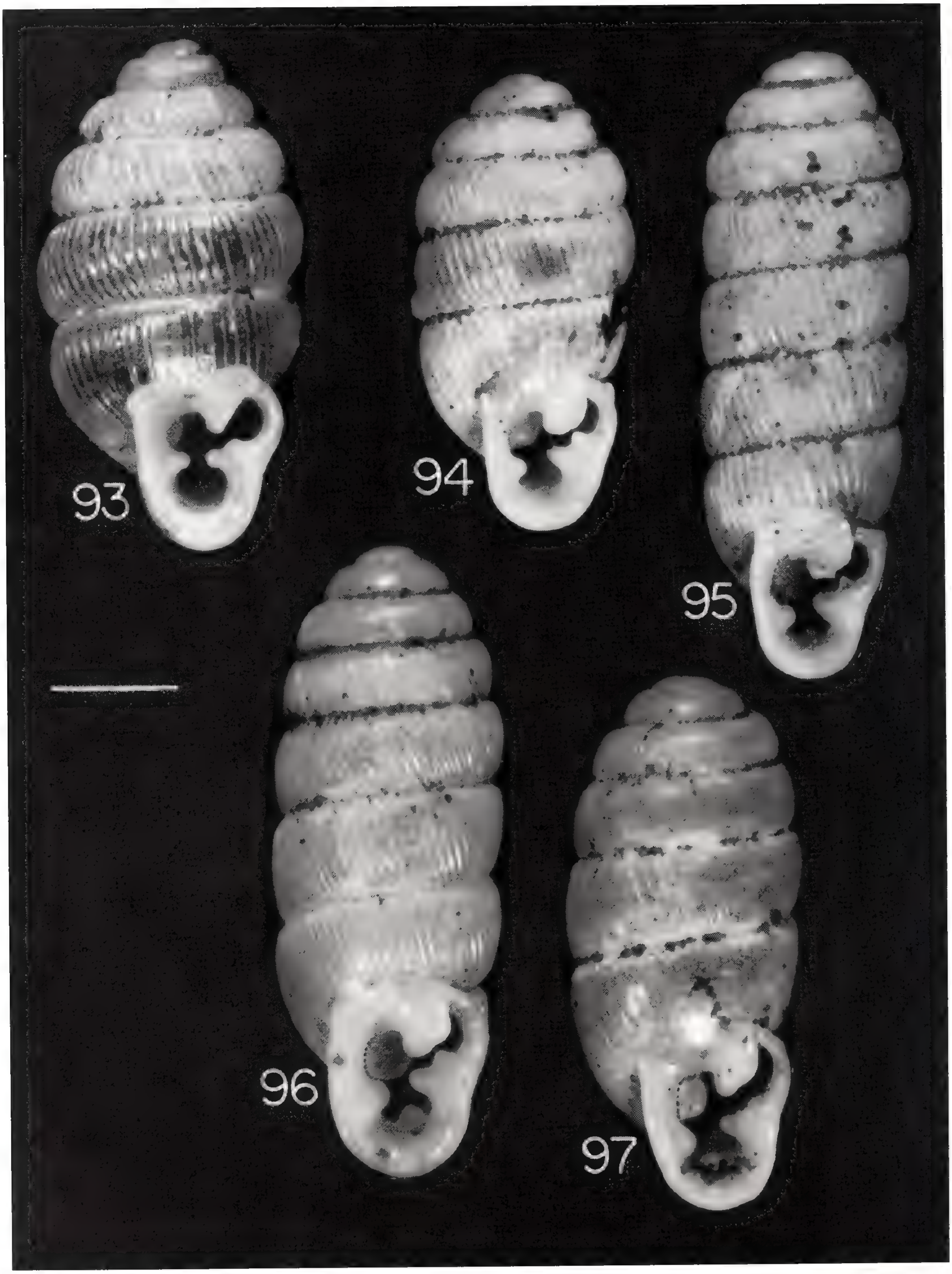
DESCRIPTION OF HOLOTYPE. Height 5.3 mm, diameter 2.4 mm (H/D 2.2), whorls 7.6 (whorls/ln height 4.55). Apical angle 100°, barreling 7.9%. Sutural depth 15.4%, sutural crenulation weak. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.93 mm, embryonic sculpture smooth. Peristome height 1.1 mm, width 0.9 mm (0.4 shell D; peristome H/W 1.2); apertural lip width 0.19 mm (0.21 peristome W). Apertural barriers consisting of a large parietal tooth; a very large palatal tooth, notched opposite the parietal tooth; (parietal-palatal embayment wide); and a moderate, deep columellar recessed baffle. Umbilicus minute.

ETYMOLOGY. For Dr. Tim Pearce, in grateful recognition of his outstanding contributions as postdoctoral associate during 1995 fieldwork and 1996 lab work.

Gulella tsaratananae sp. nov.
Figs. 27, 28

DIAGNOSIS. *G. tsaratananae* sp. nov. is somewhat similar to the Comoran *G. spreta* (Morelet, 1883) but is more loosely coiled and has a blunter apex. *G. tsaratananae* sp. nov. bears some resemblance to the Comoran *G. oryza* (Morelet, 1882) but is much more loosely coiled. *G. tsaratananae* sp. nov. is also somewhat similar to the West African *G. sulcifera* (Morelet, 1883) but is more tightly coiled and has larger apertural teeth. Two species of Madagascan *Gulella* have (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, (c) moderately strong and low-standing rib sculpture, (d) shell height generally less than 7.5 mm due to tight coiling (whorls/ln height 4.1-4.4), and (e) palatal tooth medial in position and unnotched: *G. tsaratananae* sp. nov. and *G. miaryi*. *G. tsaratananae* sp. nov. differs from *G. miaryi* in its looser coiling (whorls/ln height about 4.1 *vs.* about 4.4) and its rainforest (*vs.* dry forest) habitat.

HOLOTYPE. Station 108 (UF 275008, 1 ad): 14°01'S, 48°46'E: Madagascar: Tsaratanana Reserve, 630 m: rainforest. 17-Jun-95.



Figs. 93-97. Fig. 93. *Gulella vatosoa* sp. nov. holotype, western Masoala Peninsula. Figs. 94-97. *G. vakinifia* sp. nov.: Fig. 94 holotype, southern Bemaraha Reserve; Figs. 95-97 paratypes: Fig. 95 type locality; Fig. 96 Namoroka Reserve; Fig. 97 northern Bemaraha Reserve. Scale bar 1 mm.

FIGURED PARATYPE. Station 105 (UF 275009, 1 ad).

OTHER DRY PARATYPES. Stations 95 (UF 275017, 1 juv); 105 (UF 275021, 3 ad); 106 (13 ad, specimens lost); 107 (UF 275011, 1 ad); 108 (UF 275018, 8 ad, 2 juv; AMS C203615, 2 ad; ANSP 403460, 2 ad; MNHN, 2 ad); 110 (UF 275013, 9 ad, 2 juv); 111 (UF 275015, 3 ad, 1 juv); 112 (UF 275014, 9 ad, 1 juv); 114 (UF 275019, 9 ad, 1 juv); 502 (UF 275010, 1 ad, 1 juv); 503 (UF 275016, 13 ad, 6 juv); 537 (UF 275012, 1 ad); 538 (UF 275020, 2 ad); 540 (UF 275022, 4 ad, 2 juv).

ALCOHOL PARATYPES. Stations 105 (UF 275148, 2 ad, 1 juv); 106 (UF 275143, 2 ad); 108 (UF 275147, 9 ad); 110 (UF 275146, 2 ad); 112 (UF 275144, 2 ad); 114 (UF 275145, 2 ad, 1 juv); 115 (UF 275149, 1 ad); 540 (UF 275142, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 5.6 mm, diameter 2.3 mm (H/D 2.4), whorls 7.1 (whorls/ln height 4.14). Apical angle 80°, barreling -2.7%. Sutural depth 5.6%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.85 mm, embryonic sculpture smooth, with a possible faint trace of minute riblets. Peristome height 1.6 mm, width 1.7 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.23 mm (0.14 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For Tsaratanana Reserve.

Gulella miaryi Fischer-Piette and Bedoucha, 1964

Fischer-Piette *et al.* (1994): fig. 54

DIAGNOSIS. Two species of Madagascan *Gulella* have (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, (c) moderately strong and low-standing rib sculpture, (d) shell height generally less than 7.5 mm due to tight coiling (whorls/ln height 4.1-4.4), and (e) palatal tooth medial in position and unnotched: *G. miaryi* and *G. tsaratananae* sp. nov. *G. miaryi* differs from *G. tsaratananae* sp. nov. in its tighter coiling (whorls/ln height about 4.4 *vs.* about 4.1) and its dry forest (*vs.* rainforest) habitat.

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 5.0 mm, diameter 2.1 mm (H/D 2.4), whorls 7.0 (whorls/ln height 4.35). Apical angle 105°, barreling 3.4%. Sutural depth 5.3%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Peristome height 1.7 mm, width 1.6 mm (0.8 shell D; peristome H/W 1.1); apertural lip width 0.30 mm (0.16 peristome W). Apertural barriers consisting of a large parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment fairly wide); and a small columellar recessed baffle. Umbilicus imperforate, apparently.

Gulella zanaharyi sp. nov.

Fig. 29

DIAGNOSIS. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture weak to none, *G. zanaharyi* sp. nov. is unique in having its (a) columellar recessed baffle huge, (b) pre-apertural base angular in profile, and (c) palatal tooth massive and often with deeply internal outlier. *G. zanaharyi* sp. nov. is also unique in these characters among Madagascan *Gulella* having (a) smooth penultimate-whorl and upper-whorl sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; (c) baso-columellar tooth buttressed equally above and below; (d) whorls/ln height 4.0-4.4; and (e) diameter of first 1.5 whorls 0.9-1.0 mm.

HOLOTYPE. Station 238 (UF 275056, 1 ad): 12°00'S, 49°17'E: Madagascar: Cap d'Ambre, near Ambatojanahary, 40 m: baobab-deciduous forest. 25-Jul-95.

FIGURED PARATYPES. Stations 241 (UF 275058, 1 ad); 407 (UF 275057, 1 ad).

OTHER DRY PARATYPES. Stations 238 (UF 275064, 4 ad, 14 juv); 239 (UF 275059, 11 ad, 2 juv; AMS C203623, 1 ad; ANSP 403461, 1 ad; MNHN, 1 ad); 400 (UF 275062, 4 ad); 404 (UF uncatalogued, 2 ad, 1 juv, possibly lost); 405 (UF 275061, 4 ad, 1 juv); 407 (UF 275063, 2 ad, 1 juv).

ALCOHOL PARATYPES. Station 238 (UF 275168, 7 ad).

DESCRIPTION OF HOLOTYPE. Height 6.9 mm, diameter 2.6 mm (H/D 2.7), whorls 8.3 (whorls/ln height 4.28). Apical angle 105°, barreling 2.4%. Sutural depth 3.6%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.93 mm, embryonic sculpture smooth. Peristome height 2.1 mm, width 1.8 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.38 mm (0.20 peristome W). Pre-apertural base of shell angular in profile. Apertural barriers consisting of a massive parietal tooth; a very large, curved-triangular palatal tooth that has a deeply internal outlier (parietal-palatal embayment fairly narrow, nearly enclosed); a massive columellar recessed baffle; and a strong, recessed baso-columellar lamella. Umbilicus a small crevice.

VARIATION. See Tables 2, 3. A baso-columellar tooth is sometimes present (Figs. 79, 80).

ETYMOLOGY. For its type locality, near Ambatojanahary (Malagasy "place of the rock of God").

Gulella lohabea sp. nov.

Fig. 30

DIAGNOSIS. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) general rib sculpture weak to none, *G. lohabea* sp. nov. is unique in its large initial whorl (diameter of first 1.5 whorls about 1.3 mm *vs.* 0.8-1.1 mm) and its transverse (*vs.* spirally lamellar to nodular) palatal tooth, and is rare in having its parietal tooth joined to and continuous with the apertural lip. *G. lohabea* sp. nov. resembles *G. boucheti*, but differs in its presence (*vs.* absence) of a baso-columellar lamella and in its smaller initial whorl (diameter of first 1.5 whorls 1.28 mm *vs.* 1.35-1.36 mm).

HOLOTYPE. Station 201 (UF 274877, 1 ad): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 315 m: dry deciduous forest. 15-Jul-95.

DRY PARATYPES. Station 201 (UF 274878, 28 ad, 8 juv; AMS C203588, 1 ad; ANSP 403462, 1 ad; MNHN, 1 ad).

ALCOHOL PARATYPES. Station 201 (UF 273598, 6 ad, 3 juv).

DESCRIPTION OF HOLOTYPE. Height 6.4 mm, diameter 2.7 mm (H/D 2.4), whorls 7.1 (whorls/ln height 3.81). Apical angle 105°, barreling 8.1%. Sutural depth 4.7%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.7, diameter of first 1.5 whorls 1.28 mm, embryonic sculpture of faint growth lines and very faint spiral striae. Peristome height 2.0 mm, width 1.9 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.34 mm (0.18 peristome W). Apertural barriers consisting of a moderate parietal tooth that is joined to and continuous with the apertural lip; a moderate, transverse, broad, rounded palatal tooth (parietal-palatal embayment somewhat narrow); a small columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus a minute, very narrow crevice.

ETYMOLOGY. For the enlarged apex (Malagasy "loha" = head, "be" = big).

Gulella ankaranensis Fischer-Piette, Blanc, Blanc and Salvat, 1994

Fischer-Piette *et al.* (1994): figs. 60 (holotype) and 61-62 (paratypes)

Fig. 31 (specimen)

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture weak to none, *G. ankaranensis* is unique in its very tight coiling (whorls/ln height 5.0-5.2) and very small initial whorl (diameter of first 1.5 whorls 0.75-0.79 mm). To avoid misidentification of *G. ankaranensis* as the similar and sometimes sympatric *G. fischerpiettei* sp. nov. or *G. satisfacta*, coiling tightness and initial whorl size must be checked carefully.

FIGURED SPECIMEN. Station 558 (UF 274767, 1 ad).

OTHER DRY VOUCHER SPECIMENS. Stations 554 (UF 274768, 1 ad); 558 (UF 274770, 2 ad); 561 (UF 274773, 1 ad); 564 (UF 274772, 1 ad, 1 juv); 565 (UF 274771, 1 ad); 568 (UF 274775, 3 ad); 570 (UF 274774, 1 ad, 2 juv); 571 (UF 274769, 2 ad, 1 juv; AMS C203567, 1 ad; ANSP 403463, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 4.0 mm, diameter 1.5 mm (H/D 2.7), whorls 7.0 (whorls/ln height 5.05). Apical angle 90°, barreling 2.0%. Sutural depth 3.8%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 0.9 mm, width 1.1 mm (0.8 shell D; peristome H/W 0.8); apertural lip width 0.20 mm (0.16 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment fairly narrow); a small columellar recessed baffle; and a moderate baso-columellar lamella.

VARIATION. See Table 2.

Gulella fischerpiettei sp. nov.

Fig. 32

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture weak to none, *G. fischerpiettei* sp. nov. is intermediate between and disjunct from *G. ankaranensis* and *G. satisfacta* in both coiling tightness (whorls/ln height 4.6-4.8, *vs.* 5.0-5.2 and 4.1-4.3) and initial whorl size (diameter of first 1.5 whorls 0.80-0.90 mm, *vs.* 0.75-0.79 mm and 0.91-0.96 mm). *G. fischerpiettei* sp. nov. is otherwise very similar to both these species, and is sometimes sympatric with each. *G. fischerpiettei* sp. nov. may have a broadish, somewhat indistinct baso-columellar tooth; it then differs from other species of similar dentition in its coiling tightness and its small-to-moderate columellar recessed baffle.

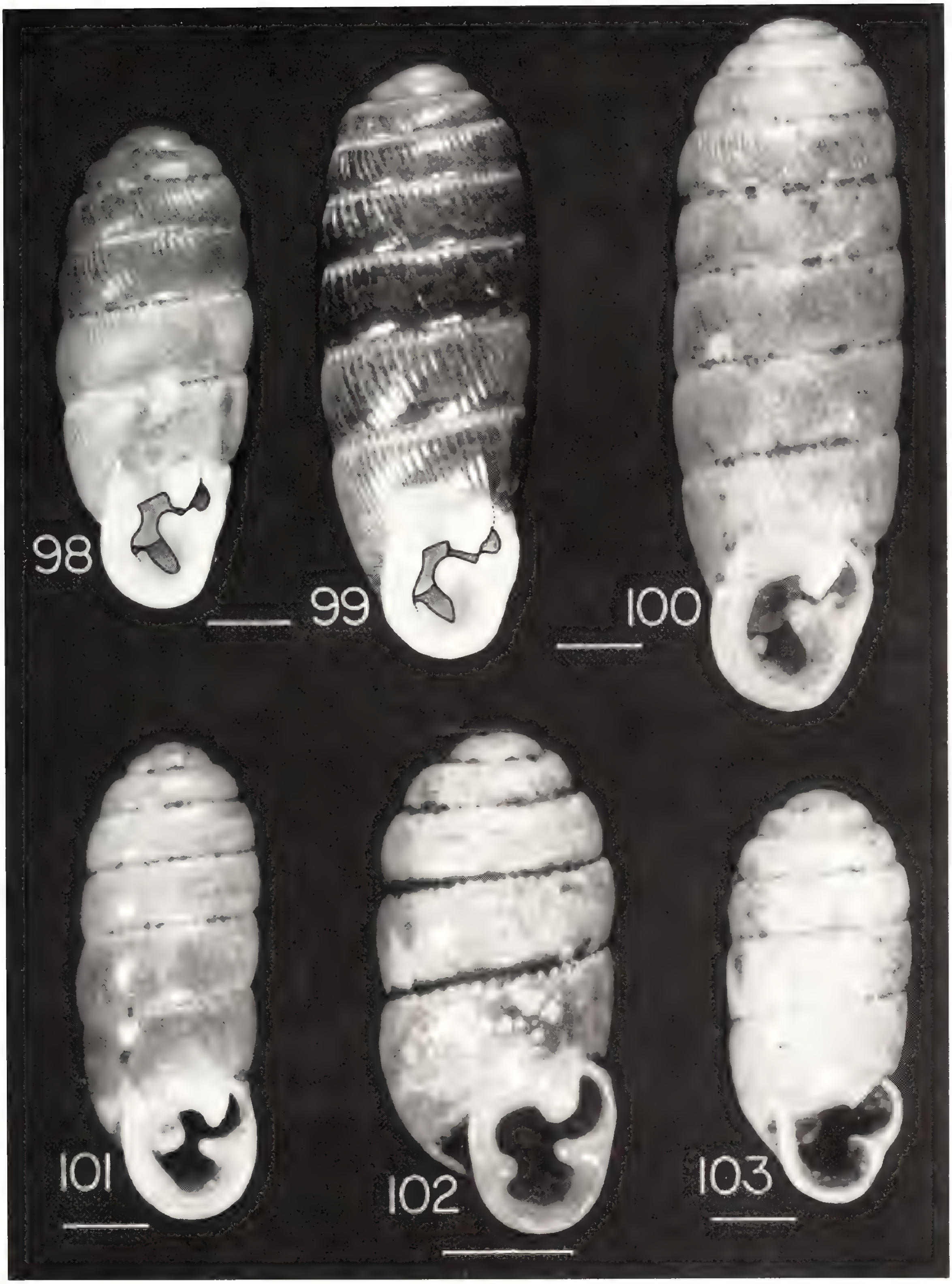
HOLOTYPE. Station 558 (UF 274824, 1 ad): 12°54'S, 49°06'E: Madagascar: Ankarana Reserve, 80 m: dry deciduous forest. 22-Aug-95.

DRY PARATYPES. Stations 558 (UF 274825, 3 ad); 803 (UF 274826, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 4.7 mm, diameter 1.8 mm (H/D 2.6), whorls 7.3 (whorls/ln height 4.69). Apical angle 115°, barreling 1.1%. Sutural depth 5.6%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.90 mm, embryonic sculpture smooth. Peristome height 1.2 mm, width 1.2 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.20 mm (0.16 peristome W). Apertural barriers consisting of a moderate parietal tooth that is separated by a groove from the apertural lip; a large, triangular palatal tooth that is nub-like and slightly recessed (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus imperforate.

VARIATION. See Tables 2, 3, 4.

ETYMOLOGY. For the late E. Fischer-Piette, monographer of the Madagascan land-snail fauna.



Figs. 98-103. Figs. 98, 99. *Gulella orchida* sp. nov.: Fig. 98 holotype, Montagne des Orchides; Fig. 99 paratype, Montagne des Français. Fig. 100. *G. magnorchida* sp. nov. holotype, southern Cap d'Ambre. Fig. 101. *G. mahia* sp. nov. paratype, northern Cap d'Ambre. Fig. 102. *G. nosybei* sp. nov. paratype, Nosy Komba. Fig. 103. *G. ambanikelia* sp. nov. neoadult paratype, type locality, Ankarana Reserve. All scale bars 1 mm.

Gulella fischerpiettei enigma subsp. nov.

Fig. 33

DIAGNOSIS. Differs from *G. fischerpiettei s.s.* sp. nov. in its smaller initial whorl (diameter of first 1.5 whorls 0.80-0.84 mm vs. 0.86-0.90 mm), its palatal tooth that is spirally lamellar and not recessed (*vs.* nub-like and slightly recessed), and its parietal tooth that is continuous with the apertural lip (*vs.* separated by a groove from the apertural lip).

HOLOTYPE. Station 816 (UF 274827, 1 ad): 12°55'S, 49°03'E: Madagascar: Ankarana Reserve, 100 m. 12-Oct-94.

DRY PARATYPES. Station 815 (UF 274828, 7 ad).

DESCRIPTION OF HOLOTYPE. Height 4.0 mm, diameter 1.7 mm (H/D 2.3), whorls 6.4 (whorls/ln height 4.58). Apical angle 90°, barreling 3.3%. Sutural depth 3.3%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.80 mm, embryonic sculpture smooth. Peristome height 1.3 mm, width 1.3 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.30 mm (0.23 peristome W). Apertural barriers consisting of a large parietal tooth that is continuous with the apertural lip; a large, triangular palatal tooth that is spirally lamellar and not recessed (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; a moderate baso-columellar lamella; and a weak baso-columellar tooth. Umbilicus a crevice.

VARIATION. See Table 4.

ETYMOLOGY. For the enigmatic size and shape, which superficially resembles an enlarged *Gulella ankaranensis*.

Gulella satisfacta Fischer-Piette, Blanc, Blanc and Salvat, 1994

Figs. 36, 37, 38

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture weak to none, *G. satisfacta* is unique in its combination of (a) broadly rounded, non-tooth-like columellar recessed baffle; (b) diameter of first 1.5 whorls 0.91-0.96; and (c) whorls/ln height 4.09-4.30. *G. satisfacta* is not known outside Ankarana Reserve and adjacent karst, where it is sometimes sympatric with either *G. ankaranensis* or *G. fischerpiettei* sp. nov. It shares its broadly rounded, non-tooth-like columellar recessed baffle with these two species, but differs from them in its looser coiling (whorls/ln height 4.09-4.30 *vs.* 4.6-5.2) and larger initial whorl (diameter of first 1.5 whorls 0.91-0.96 *vs.* 0.75-0.90 mm). Three species of southern Cap d'Ambre (*G. mahia* sp. nov., *G. ranomasina* sp. nov., and *G. jaominai* sp. nov.) can overlap or approach *G. satisfacta* in coiling tightness and/or initial-whorl size, but differ from it in their nubbed, toothlike columellar recessed baffles.

FIGURED SPECIMENS. Stations 564 (UF 274993, 1 ad); 576 (UF 274991, 1 ad); 577 (UF 274992, 1 ad).

OTHER DRY VOUCHER SPECIMENS. Stations 564 (UF 274995, 12 ad, 4 juv); 570 (UF 274994, 2 juv); 576 (UF 274997, 2 ad, 1 juv); 577 (UF 274996, 5 ad, 1 juv).

ALCOHOL VOUCHER SPECIMENS. Station 564 (UF 275139, 2 ad, 1 juv).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 6.2 mm, diameter 2.4 mm (H/D 2.6), whorls 7.5 (whorls/ln height 4.11). Apical angle 80o, barreling 7.6%. Sutural depth 7.8%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 1.5 mm, width 1.7 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.21 mm (0.12 peristome W). Apertural barriers consisting of a large parietal tooth; a large, rounded-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a strong baso-columellar lamella.

VARIATION. See Tables 2, 3, 4.

Gulella satisfacta charlesblanci subsp. nov.

Fig. 34

DIAGNOSIS. Differs from both *G. satisfacta s.s.* and *G. s. vitsia* subsp. nov. in its tighter coiling (whorls/ln height 4.30 *vs.* 4.09-4.21) and its presence (*vs.* absence) of a small baso-columellar tooth. It further differs from *G. s. vitsia* subsp. nov. in its smooth (*vs.* weakly ribbed) sculpture and its large (*vs.* extremely large) baso-columellar lamella. *G. s. charlesblanci* subsp. nov. differs from other species of similar, tridentate dentition in its coiling tightness and its small-to-moderate columellar recessed baffle.

HOLOTYPE. Station 571 (UF 274989, 1 ad): 12°57'S, 49°07'E: Madagascar: Ankarana Reserve, 85 m: dry deciduous forest. 24-Aug-95.

DESCRIPTION OF HOLOTYPE. Height 4.8 mm, diameter 1.8 mm (H/D 2.6), whorls 6.7 (whorls/ln height 4.30). Apical angle 85°, barreling 4.2%. Sutural depth 8.5%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Diameter of first 1.5 whorls 0.95 mm. Peristome height 1.3 mm, width 1.3 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.28 mm (0.19 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; a strong baso-columellar lamella; and a weak baso-columellar tooth.

ETYMOLOGY. For Charles P. Blanc, co-monographer of Madagascan land snails.

Gulella satisfacta vitsia subsp. nov.

Fig. 35

DIAGNOSIS. Differs from both *G. satisfacta s.s.* and *G. s.*

charlesblanci subsp. nov. in its weakly ribbed (*vs.* smooth) sculpture and its baso-columellar lamella that is massive and extends upward to near the columellar insertion (*vs.* strong but not approaching the columellar insertion). Further differs from *G. s. charlesblanci* subsp. nov. in its looser coiling (whorls/ln height 4.09-4.21 vs. 4.30) and its absence (*vs.* presence) of a small baso-columellar tooth.

HOLOTYPE. Station 810 (UF 274998, 1 ad): 12°54'S, 49°06'E: Madagascar: Ankarana Reserve, 90 m. 10-Oct-94.

ALCOHOL PARATYPE. Station 810 (UF 275140, 1 ad)

DESCRIPTION OF HOLOTYPE. Height 5.1 mm, diameter 1.9 mm (H/D 2.7), whorls 6.8 (whorls/ln height 4.18). Apical angle 100°, barreling 1.7%. Sutural depth 6.5%, sutural crenulation strong. In apertural view, penultimate and body whorls with weak rib sculpture that does not diminish in strength toward the lower suture. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.95 mm, embryonic sculpture smooth. Peristome height 1.6 mm, width 1.4 mm (0.8 shell D; peristome H/W 1.1); apertural lip width 0.23 mm (0.16 peristome W). Apertural barriers consisting of a large parietal tooth; a large, rounded-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a very strong baso-columellar lamella, extending upward to near the columellar insertion. Umbilicus a crevice.

ETYMOLOGY. For the seeming rarity (Malagasy "vitsy" = rare) of the taxon, known from a single specimen.

Gulella mahia sp. nov.

Figs. 39, 40, 101

DIAGNOSIS. There are three species of Madagascan Gulella having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) general rib sculpture weak to none, (d) whorls/ln height 3.9-4.4, (e) diameter of first 1.5 whorls 0.88-1.02 mm, and (e) columellar recessed baffle nubbed and tooth-like: *G. mahia* sp. nov., *G. ranomasina* sp. nov., and *G. jaominai* sp. nov. *G. mahia* sp. nov. differs from the latter two in its larger initial whorl (diameter of first 1.5 whorls 0.98-1.02 mm *vs.* 0.88-0.93 mm) and its intermediate coiling tightness (whorls/ln height 4.1 *vs.* 4.2-4.4 and 3.9-4.0). *G. mahia* sp. nov. is sometimes sympatric with *G. ranomasina* sp. nov., from which it further differs in the convex (*vs.* concave) sides of its shell. *G. mahia* sp. nov. differs from *G. satisfacta* in its nubbed and toothlike (*vs.* broadly rounded and non-toothlike) baso-columellar lamella and in its larger initial whorl size (diameter of first 1.5 whorls 0.975-1.025 mm *vs.* 0.913-0.962 mm).

HOLOTYPE. Station 400 (UF 274902, 1 ad): 12°10'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 70 m: dry deciduous forest. 24-Aug-95.

FIGURED PARATYPES. Stations 239 (UF 274904, 1 ad); 400 (UF 274903, 1 ad).

OTHER DRY PARATYPES. Stations 400 (UF 274905, 1 juv); 403 (AMS C203595, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.0 mm, diameter 2.1 mm (H/D 2.4), whorls 6.6 (whorls/ln height 4.09). Apical angle 90°, barreling 4.5%. Sutural depth 4.5%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.99 mm, embryonic sculpture smooth. Peristome height 1.4 mm, width 1.5 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.25 mm (0.17 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate, triangular columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus an extremely minute crevice.

VARIATION. See Table 2.

ETYMOLOGY. For its shape, which superficially resembles an emaciated (Malagasy "mahia") version of *Gulella ambrensis capdambri* subsp. nov., with which it is sometimes sympatric.

Gulella ranomasina sp. nov.

Fig. 41

DIAGNOSIS. There are three species of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) general rib sculpture weak to none, (d) whorls/ln height 3.9-4.4, (e) diameter of first 1.5 whorls 0.88-1.02 mm, and (e) columellar recessed baffle nubbed and tooth-like: *G. ranomasina* sp. nov., *G. jaominai* sp. nov., and *G. mahia* sp. nov. *G. ranomasina* sp. nov. differs from the latter two in the concave (*vs.* convex) sides of its shell, and further differs from *G. jaominai* sp. nov. in its tighter coiling (whorls/ln height 4.22-4.40 *vs.* 3.90-3.98). *G. ranomasina* sp. nov. is sometimes sympatric with *G. mahia* sp. nov., from which it further differs in both its smaller initial whorl (diameter of first 1.5 whorls 0.875-0.932 mm *vs.* 0.975-1.025 mm) and its tighter coiling (whorls/ln height 4.22-4.40 *vs.* 4.07-4.12). *G. ranomasina* sp. nov. differs from *G. satisfacta* in its nubbed and toothlike (*vs.* broadly rounded and non-toothlike) baso-columellar lamella and in its concave-sided shell.

HOLOTYPE. Station 241 (UF 274982, 1 ad): 12°00'S, 49°17'E: Madagascar: Cap d'Ambre, near Ambatojanahary, 15 m: dry deciduous forest. 25-Jul-95.

DRY PARATYPES. Stations 238 (UF 274983, 8 ad, 2 juv; AMS C203609, 1 ad; ANSP 403464, 1 ad; MNHN, 1 ad); 239 (UF 274984, 3 ad, 1 juv); 240 (UF 274985, 3 ad).

ALCOHOL PARATYPES. Stations 239 (UF 275138, 1 ad); 240 (UF 275137, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.3 mm, diameter 1.8 mm (H/D 2.9), whorls 7.2 (whorls/ln height 4.31).

Apical angle 95°, barreling 0.0%. Sutural depth 6.7%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.8, diameter of first 1.5 whorls 0.88 mm, embryonic sculpture smooth. Peristome height 1.5 mm, width 1.4 mm (0.8 shell D; peristome H/W 1.1); apertural lip width 0.25 mm (0.18 peristome W). Apertural barriers consisting of a large parietal tooth; a moderate, peg-shaped palatal tooth with a broad triangular base (parietal-palatal embayment somewhat narrow); a moderate, nubbed columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus an extremely small crevice.

VARIATION. See Table 2.

ETYMOLOGY. For the ocean water (Malagasy "ranomasina") near the type locality.

Gulella jaominai sp. nov.

Fig. 42

DIAGNOSIS. There are three species of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) general rib sculpture weak to none, (d) whorls/ln height 3.9-4.4, (e) diameter of first 1.5 whorls 0.88-1.02 mm, and (e) columellar recessed baffle nubbed and tooth-like: *G. jaominai* sp. nov., *G. ranomasina* sp. nov., and *G. mahia* sp. nov. *G. jaominai* sp. nov. differs from *G. ranomasina* sp. nov. in its looser coiling (whorls/ln height 3.90-3.98 *vs.* 4.22-4.40) and its straight- to convex-sided (*vs.* concave-sided) shell. *G. jaominai* sp. nov. differs from *G. mahia* in its smaller initial whorl (diameter of first 1.5 whorls 0.91-0.94 mm *vs.* 0.98-1.02 mm) and its looser coiling (whorls/ln height 3.90-3.98 *vs.* 4.07-4.12). *G. jaominai* sp. nov. differs from *G. satisfacta* in its nubbed and toothlike (*vs.* broadly rounded and non-toothlike) baso-columellar lamella and in its looser coiling (whorls/ln height 3.90-3.98 *vs.* 4.09-4.30).

HOLOTYPE. Station 401 (UF 274849, 1 ad): 12°11'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 205 m: dry deciduous-baobab forest. 24-Aug-95.

DRY PARATYPES. Stations 401 (UF 274850, 1 ad, 2 juv); 404 (UF 274851, 4 ad, 4 juv).

ALCOHOL PARATYPES. Station 404 (UF 275068, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 6.1 mm, diameter 2.4 mm (H/D 2.5), whorls 7.1 (whorls/ln height 3.94). Apical angle 110°, barreling 1.6%. Sutural depth 8.4%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.94 mm, embryonic sculpture smooth. Peristome height 1.7 mm, width 1.7 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.36 mm (0.21 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Table 2.

ETYMOLOGY. For Jaomina, teacher in Diego Suarez, uncle of the author, and co-collector of this species.

Gulella ambrensis sp. nov.

Fig. 43

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) general rib sculpture weak to none, and (d) palatal tooth spirally lamellar to nodular, *G. ambrensis* sp. nov. is unique in its combination of loose coiling (whorls/ln height 3.68-3.98) and large initial whorl (diameter of first 1.5 whorls 1.02-1.17 mm). Within this group, its coiling is approached only by *G. jaominai* sp. nov. (whorls/ln height 3.90-3.98), which has a much smaller initial whorl (diameter of first 1.5 whorls 0.912-0.938 mm); and its large initial whorl is approached only by *G. mahia* sp. nov., which has tighter coiling (whorls/ln height 4.07-4.12).

HOLOTYPE. Station 181 (UF 274659, 1 ad): 12°37'S, 49°10'E: Madagascar: Montagne d'Ambre National Park, 1040 m: rainforest. 9-Jul-95.

DRY PARATYPES. Stations 170 (UF 274667, 12 ad, 1 juv); 172 (UF 274665, 11 ad, 1 juv); 178 (UF 274666, 1 ad); 181 (UF 274660, 12 ad, 4 juv; AMS C203564, 1 ad; ANSP 403465, 1 ad; MNHN, 1 ad); 182 (UF 274664, 2 ad, 2 juv); 184 (UF 274668, 1 ad); 185 (UF 274662, 3 ad); 192 (UF 274663, 6 ad, 1 juv); 193 (UF 274661, 1 ad); 195 (UF 274669, 41 ad, 9 juv).

ALCOHOL PARATYPES. Stations 172 (UF 273663, 1 ad, 1 juv); 178 (UF 273658, 1 ad); 181 (UF 273662, 6 ad, 1 juv); 182 (UF 273661, 2 ad, 1 juv); 192 (UF 273664, 2 juv); 193 (UF 273659, 1 juv); 195 (UF 273655, 6 ad, 1 juv).

DESCRIPTION OF HOLOTYPE. Height 6.3 mm, diameter 2.8 mm (H/D 2.3), whorls 7.1 (whorls/ln height 3.81). Apical angle 105°, barreling 3.5%. Sutural depth 3.6%, sutural crenulation weak. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 1.04 mm, embryonic sculpture virtually smooth. Peristome height 2.0 mm, width 1.9 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.34 mm (0.18 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate, nubbed columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Tables 3, 4.

ETYMOLOGY. For Montagne d'Ambre National Park.

Gulella ambrensis andavakoerae subsp. nov.

Fig. 44

DIAGNOSIS. Known only from the Andavakoera massif, north of Betsiaka. Differs from *G. ambrensis s.s.* sp. nov. in its larger initial whorl (diameter of first 1.5 whorls 1.075-1.100 mm *vs.* 1.025-1.050 mm), strong (*vs.* weak) sutural crenulation, deciduous-forest (*vs.* rainforest) habitat, and extension of the palatal-tooth lamella all the way to (*vs.* stopping before) the apertural-lip edge. Differs from *G. a. capdambri* subsp. nov. in its non-recessed (*vs.* often recessed) palatal tooth and in the extension of its palatal-tooth lamella all the way to (*vs.* stopping before) the apertural-lip edge. Differs from *G. a. orangea* subsp. nov. in its larger initial whorl (diameter of first 1.5 whorls 1.075-1.100 mm *vs.* 1.025-1.038 mm) and in the extension of its palatal-tooth lamella all the way to (*vs.* stopping before) the apertural-lip edge. Differs from *G. a. rakotomalalai* subsp. nov. in its smaller initial whorl (diameter of first 1.5 whorls 1.075-1.100 mm vs. 1.150-1.168 mm).

HOLOTYPE. Station 417 (UF 274670, 1 ad): 13°06'S, 49°13'E: Madagascar: Andavakoera, N of Betsiaka, 230 m: dry deciduous forest. 30-Aug-95.

OTHER DRY PARATYPES. Stations 413 (UF 274672, 1 juv); 417 (UF 274674, 28 ad, 10 juv); 418 (UF 274673, 37 ad, 18 juv); 421 (UF 274675, 3 ad, 4 juv; UF 274671, 1 ad).

ALCOHOL PARATYPES. Stations 413 (UF 273657, 2 ad, 1 juv); 417 (UF 273660, 2 ad); 418 (UF 273656, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 5.9 mm, diameter 2.8 mm (H/D 2.1), whorls 6.5 (whorls/ln height 3.68). Apical angle 95°, barreling 3.5%. Sutural depth 6.0%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 1.08 mm, embryonic sculpture smooth. Peristome height 2.1 mm, width 1.9 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.38 mm (0.17 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Table 4.

ETYMOLOGY. For the Andavakoera massif, north of Betsiaka.

Gulella ambrensis rakotomalalai subsp. nov.

Fig. 45

DIAGNOSIS. Known only from Analamera Reserve. Differs from *G. ambrensis s.s.* sp. nov., *G. a. andavakoerae* subsp. nov., and both other subspecies of *G. ambrensis* sp. nov. in its larger initial whorl (diameter of first 1.5 whorls 1.150-1.168 mm *vs.* 1.025-1.100 mm). Further differs from *G. ambrensis s.s.* sp. nov. in its strong (*vs.* weak) sutural crenulation, deciduous-forest (*vs.* rainforest) habitat, and extension of the palatal-tooth lamella all the way to (*vs.* stopping before) the apertural-lip edge. Further differs from *G. a. capdambri* subsp. nov. in its non-recessed (*vs.* often recessed) palatal tooth. Further differs from *G. a. orangea* subsp. nov. in its looser coiling (whorls/ln height 3.76-3.87 *vs.* 3.88-3.98) and in the extension of its palatal-tooth lamella all the way to (*vs.* stopping before) the apertural-lip edge.

HOLOTYPE. Station 208 (UF 274648, 1 ad): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 100 m: dry deciduous forest. 16-Jul-95.

DRY PARATYPES. Stations 204 (UF 274651, 1 juv); 206 (UF 274650, 1 ad, 1 juv); 208 (UF 274653, 2 ad); 210 (UF 274649, 2 ad, 1 juv); 213 (UF 274652, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 6.0 mm, diameter 2.5 mm (H/D 2.4), whorls 6.7 (whorls/ln height 3.76). Apical angle 95°, barreling 5.0%. Sutural depth 9.0%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.8, diameter of first 1.5 whorls 1.17 mm, embryonic sculpture smooth, with a trace of sutural notches. Peristome height 1.8 mm, width 1.8 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.26 mm (0.14 peristomeW). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Table 4.

ETYMOLOGY. In honor of the late Max Felix Rakotomalala, assistant and friend.

Gulella ambrensis capdambri subsp. nov.

Fig. 46

DIAGNOSIS. Known only from Cap d'Ambre. Differs from *G. ambrensis s.s.* sp. nov. and all other subspecies of *G. ambrensis* sp. nov. in its often recessed (*vs.* non-recessed) palatal tooth. Further differs from *G. ambrensis s.s.* sp. nov. in its strong (*vs.* weak) sutural crenulation and deciduous-forest (*vs.* rainforest) habitat. Further differs from *G. a. andavakoerae* subsp. nov. in its palatal-tooth lamella stopping before (*vs.* extending all the way to) the apertural-lip edge. Further differs from *G. a. orangea* subsp. nov. in its larger initial whorl (diameter of first 1.5 whorls 1.058-1.100 mm *vs.* 1.025-1.038 mm). Further differs from *G. a. rakotomalalai* subsp. nov. in its smaller initial whorl (diameter of first 1.5 whorls 1.025-1.038 mm *vs.* 1.150-1.168 mm).

HOLOTYPE. Station 230 (UF 274688, 1 ad): 11°57'S, 49°16'E: Madagascar: Cap d'Ambre, near lighthouse, 20 m: dry deciduous forest. 24-Jul-95.

DRY PARATYPES. Stations 230 (UF 274691, 6 ad, 2 juv); 233 (UF 274692, 22 ad, 5 juv; AMS C203574, 1 ad; ANSP 403466, 1 ad; MNHN, 1 ad); 238 (UF 274690, 1 ad, 3 juv); 240 (UF 274689, 2 ad, 1 juv).

ALCOHOL PARATYPES. Station 230 (UF 275066, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 6.8 mm, diameter 3.0 mm (H/D 2.3), whorls 7.4 (whorls/ln height 3.86).

Apical angle 115°, barreling 6.3%. Sutural depth 4.2%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.06 mm, embryonic sculpture smooth. Peristome height 2.3 mm, width 2.0 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.44 mm (0.22 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate, slightly nubbed columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Tables 2, 4.

ETYMOLOGY. For Cap d'Ambre, NW of Diego Suarez.

Gulella ambrensis orangea subsp. nov.

Fig. 47

DIAGNOSIS. Known only from Forêt d'Orange, Cap Mine. Differs from *G. ambrensis s.s.* sp. nov. in its strong (*vs.* weak) sutural crenulation and its deciduous-forest (*vs.* rainforest) habitat. Differs from all other subspecies except *G. ambrensis s.s.* sp. nov. in its smaller initial whorl (diameter of first 1.5 whorls 1.025-1.038 mm *vs.* 1.058-1.168 mm). Further differs from *G. a. andavakoerae* subsp. nov. in its palatal-tooth lamella stopping before (*vs.* extending all the way to) the apertural-lip edge. Further differs from *G. a. capdambri* subsp. nov. in its non-recessed (*vs.* often recessed) palatal tooth. Further differs from *G. a. rakotomalalai* subsp. nov. in its tighter coiling (whorls/ln height 3.88-3.98 *vs.* 3.76-3.87) and in its palatal-tooth lamella stopping before (*vs.* extending all the way to) the apertural-lip edge.

HOLOTYPE. Station 225 (UF 274645, 1 ad): 12°14'S, 49°22'E: Madagascar: Forêt d'Orange, Baie des Dunes, Cap Mine, 6 m: scrub. 21-Jul-95.

DRY PARATYPES. Stations 224 (UF 274646, 8 ad, 4 juv; AMS C203603, 1 ad; ANSP 403467, 1 ad; MNHN, 1 ad); 225 (UF 274647, 1 ad).

ALCOHOL PARATYPES. Station 224 (UF 275067, 3 ad).

DESCRIPTION OF HOLOTYPE. Height 6.1 mm, diameter 2.4 mm (H/D 2.5), whorls 7.2 (whorls/ln height 3.97). Apical angle 90°, barreling 3.8%. Sutural depth 4.0%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.8, diameter of first 1.5 whorls 1.03 mm, embryonic sculpture smooth, with a trace of sutural notches. Peristome height 1.9 mm, width 1.8 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.34 mm (0.19 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate, nubbed columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Tables 2, 4.

ETYMOLOGY. For Forêt d'Orange, Cap Mine, NE of Diego Suarez.

Gulella bemarahae sp. nov.

Fig. 49

DIAGNOSIS. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture strong to moderate, in only two species does the rib sculpture continue undiminished from the upper to the lower suture: *G. bemarahae* sp. nov. and *G. nakamaroa* sp. nov. *G. bemarahae* sp. nov. differs from *G. nakamaroa* sp. nov. in its palatal tooth that is transverse and squarish (*vs.* a short spiral lamella that is triangular in apertural view); looser coiling (whorls/ln height about 3.65 *vs.* about 3.85); smaller initial whorl (diameter of first 1.5 whorls about 1.2 mm *vs.* about 1.3 mm); and columnar (*vs.* barreled) shell shape. *G. bemarahae* sp. nov. is more tightly coiled than either *G. josephinae* sp. nov. or *G. soulaiana* (whorls/ln height 3.65 *vs.* 3.2 and 3.4), and has a larger initial whorl than *G. rugosa* sp. nov. (diameter of first 1.5 whorls about 1.2 *vs.* about 1.0); it also has a strong baso-columellar lamella that is lacking or weak in those other species.

HOLOTYPE. Station 249 (UF 274798, 1 ad): 19°08'S, 44°50'E: Madagascar: Bemaraha Reserve, 100 m: tall riverine gallery forest. 16-Jun-95.

DRY PARATYPES. Stations 248 (UF 274799, 7 ad, 6 juv); 249 (UF 274800, 8 ad, 31 juv; AMS C203570, 5 ad, 10 juv; ANSP 403468, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 9.4 mm, diameter 3.0 mm (H/D 3.1), whorls 8.2 (whorls/ln height 3.66). Apical angle 100°, barreling 3.3%. Sutural depth 5.0%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.7, diameter of first 1.5 whorls 1.20 mm, embryonic sculpture of extremely faint growth lines. Peristome height 2.5 mm, width 2.5 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.45 mm (0.18 peristome W). Apertural barriers consisting of a large parietal tooth; a large, squarish palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

ETYMOLOGY. For Bemaraha Reserve.

Gulella nakamaroa sp. nov.

Fig. 50

DIAGNOSIS. *G. nakamaroa* sp. nov. is somewhat similar to the West African *G. sulcifera* (Morelet, 1883) but has much stronger apertural dentition and an angular instead of a rounded columellar insertion. *G. nakamaroa* sp. nov.

bears some resemblance to the West African *G. circumcisa* (Morelet, 1885) but has looser coiling, a much stronger palatal tooth, and an angular instead of a rounded columellar insertion. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture strong to moderate, in only two species does the rib sculpture continue undiminished from the upper to the lower suture: *G. nakamaroa* sp. nov. and *G. bemarahae* sp. nov. *G. nakamaroa* sp. nov. differs from *G. bemarahae* sp. nov. in its palatal tooth that is a short spiral lamella appearing triangular in apertural view (*vs.* transverse and squarish); tighter coiling (whorls/ln height about 3.85 *vs.* about 3.65); larger initial whorl (diameter of first 1.5 whorls about 1.3 mm *vs.* about 1.2 mm); and barreled (*vs.* columnar) shell shape. *G. nakamaroa* sp. nov. differs rather markedly from all other two-toothed, ribbed, Madagascan species of *Gulella*.

HOLOTYPE. Station 805 (UF 274959, 1 ad): 13°01'S, 49°00'E: Madagascar: Ankarana Reserve, 50 m. 8-Oct-94.

DRY PARATYPES. Station 805 (UF 274960, 22 ad, 17 juv; AMS C203601, 22 ad, 17 juv; ANSP 403469, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 8.7 mm, diameter 3.7 mm (H/D 2.4), whorls 8.3 (whorls/ln height 3.84). Apical angle 90°, barreling 6.8%. Sutural depth 5.4%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.0, diameter of first 1.5 whorls 1.28 mm, embryonic sculpture of minute riblets. Peristome height 2.6 mm, width 2.5 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.55 mm (0.22 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus imperforate.

ETYMOLOGY. For the many (Malagasy "maro") specimens taken (Malagasy "naka") at the single known locality.

Gulella capmini sp. nov.

Figs. 48, 51

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) strong-to-moderate rib sculpture that diminishes conspicuously between the upper and lower sutures, *G. capmini* sp. nov. is unique both in having its columellar recessed baffle conspicuous, nubbed, and toothlike; and in having the palatal tooth recessed about as deeply as the recessed columellar baffle. *G. capmini* sp. nov. occurs sympatrically with *G. ambrensis orangea* subsp. nov., which is superficially similar but has smooth sculpture, looser coiling, and a larger initial whorl.

HOLOTYPE. Station 225 (UF 274815, 1 ad): 12°14'S, 49°22'E: Madagascar: Baie des Dunes, Cap Mine, 6 m: scrub. 21-Jul-95.

DRY PARATYPES. Stations 224 (UF 274817, 3 ad, 2 juv); 225 (UF 274816, 7 ad, 1 juv; AMS C203575, 1 ad; ANSP 403470, 1 ad; MNHN, 1 ad).

ALCOHOL PARATYPES. Station 224 (UF 275084, 3 ad)

DESCRIPTION OF HOLOTYPE. Height 4.8 mm, diameter 2.5 mm (H/D 1.9), whorls 6.8 (whorls/ln height 4.33). Apical angle 120°, barreling 0.0%. Sutural depth 3.7%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.2, diameter of first 1.5 whorls 1.08 mm, embryonic sculpture smooth. Peristome height 1.5 mm, width 1.7 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.25 mm (0.15 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, rounded palatal tooth (parietal-palatal embayment moderately wide); a moderate, rather shallowly recessed columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Tables 2, 3.

ETYMOLOGY. For Cap Mine, E of Diego Suarez.

Gulella marojejyae sp. nov.

Fig. 52

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) strong-to-moderate rib sculpture that diminishes conspicuously between the upper and lower sutures, (d) columellar recessed baffle inconspicuous, broadly rounded, and not toothlike, and (e) palatal tooth much shallower than the recessed columellar baffle, *G. marojejyae* sp. nov. is unique in its large, loosely coiled shell (whorls/ln height about 3.3-3.4 *vs.* 4.1-4.6, diameter of first 1.5 whorls 1.0-1.1 mm *vs.* 0.8-0.9 mm). *G. marojejyae* sp. nov. is somewhat similar to *G. masoalae* sp. nov. in size, coiling, and apertural dentition, but is smaller in initial whorl (diameter of first 1.5 whorls 1.0-1.1 mm *vs.* 1.25-1.35 mm) and has half-ribbed (*vs.* smooth) sculpture. *G. marojejyae* sp. nov. bears some resemblance to *G. michellae* sp. nov., with which it is sometimes sympatric but from which it differs in its diminished (*vs.* undiminished) ribbing, its absence (*vs.* presence) of a baso-columellar tooth, and its much looser coiling (whorls/ln height 3.3 vs. 4.0).

HOLOTYPE. Station 649 (UF 274920, 1 ad): 14°29'S, 49°34'E: Madagascar: W Marojejy Reserve, 700 m: rainforest. 28-Sep-95.

DRY PARATYPES. Stations 612 (UF 274922, 1 juv); 645 (UF 274927, 2 ad); 648 (UF 274921, 1 ad); 649 (UF 274926, 2 ad, 1 juv; AMS C203597, 1 ad; ANSP 403471, 1 ad; MNHN, 1 ad); 650 (UF 274923, 1 ad); 679 (UF

274925, 1 ad); 680 (UF 274924, 1 ad).

ALCOHOL PARATYPES. Stations 627 (UF 275128, 1 ad); 645 (UF 275127, 1 juv); 649 (UF 275126, 1 ad); 650 (UF 275125, 2 juv).

DESCRIPTION OF HOLOTYPE. Height 7.0 mm, diameter 3.2 mm (H/D 2.2), whorls 6.5 (whorls/ln height 3.34). Apical angle 85°, barreling 0.0%. Sutural depth 4.9%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.16 mm, embryonic sculpture smooth, with faint traces of minute riblets. Peristome height 2.4 mm, width 2.2 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.41 mm (0.19 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, broad, rounded, evenly buttressed palatal tooth (parietal-palatal embayment fairly narrow); a small columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus an extremely minute, narrow crevice.

ETYMOLOGY. For Marojejy Reserve.

Gulella griffithsi sp. nov.

Fig. 53

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) strong-to-moderate rib sculpture that diminishes conspicuously between the upper and lower sutures, (d) columellar recessed baffle inconspicuous, broadly rounded, and not toothlike, and (e) palatal tooth much shallower than the recessed columellar baffle, only two species have a small and tightly coiled shell (whorls/ln height about 4.1-4.6, diameter of first 1.5 whorls 0.8-0.9 mm): *G. griffithsi* sp. nov. and *G. tsara* sp. nov. *G. griffithsi* sp. nov. differs from *G. tsara* sp. nov. in its much looser coiling (whorls/ln height about 4.1-4.2 *vs.* 4.5-4.6), its large (*vs.* moderate) parietal tooth, and its deciduous-forest (*vs.* rainforest) habitat.

HOLOTYPE. Station 247 (UF 274834, 1 ad, 1 juv): 19°08'S, 44°52'E: Madagascar: S Bemaraha Reserve, 100 m: lush tall riverine gallery forest. 15-Jun-95.

DRY PARATYPES. Stations 247 (UF 274835, 1 ad; AMS C203580, 1 ad; ANSP 403472, 1 ad; MNHN, 1 ad); 489 (UF 274836, 1 ad, 1 juv; AMS C203581, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 4.4 mm, diameter 1.9 mm (H/D 2.4), whorls 6.3 (whorls/ln height 4.23). Apical angle 85°, barreling 0.0%. Sutural depth 6.0%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 1.8, diameter of first 1.5 whorls 0.84 mm, embryonic sculpture smooth. Peristome height 1.4 mm, width 1.5 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.22 mm (0.15 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus a crevice.

ETYMOLOGY. For Owen Griffiths, the collector.

Gulella tsara sp. nov.

Fig. 54

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) strong-to-moderate rib sculpture that diminishes conspicuously between the upper and lower sutures, (d) columellar recessed baffle inconspicuous, broadly rounded, and not toothlike, and (e) palatal tooth much shallower than the recessed columellar baffle, only two species have a small and tightly coiled shell (whorls/ln height about 4.1-4.6, diameter of first 1.5 whorls 0.8-0.9 mm): *G. tsara* sp. nov. and *G. griffithsi* sp. nov. *G. tsara* sp. nov. differs from *G. griffithsi* sp. nov. in its much tighter coiling (whorls/ln height about 4.5-4.6 *vs.* 4.1-4.2), its moderate (*vs.* large) parietal tooth, and its rainforest (*vs.* deciduous-forest) habitat.

HOLOTYPE. Station 513 (UF 275000, 1 ad): 13°59'S, 48°47'E: Madagascar: Tsaratanana Reserve, 1525 m: rainforest. 14-Jun-95.

DRY PARATYPES. Stations 505 (AMS C203614, 1 ad); 513 (UF 275003, 1 juv); 514 (UF 275001, 1 juv); 527 (UF 275002, 1 ad, 1 juv); 535 (ANSP 403473, 1 ad; MNHN, 1 ad).

ALCOHOL PARATYPE. Station 95 (UF 275141, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.8 mm, diameter 1.9 mm (H/D 2.0), whorls 6.1 (whorls/ln height 4.55). Apical angle 85°, barreling 1.1%. Sutural depth 4.4%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 1.8, diameter of first 1.5 whorls 0.88 mm, embryonic sculpture smooth, with a trace of minute riblets. Peristome height 1.2 mm, width 1.3 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.20 mm (0.16 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus a small crevice.

ETYMOLOGY. Both for its resemblance to a smaller version of *Gulella tsaratananae* sp. nov. and for its pleasing (Malagasy "tsara") appearance.

Gulella microstriata sp. nov.

Fig. 55

DIAGNOSIS. Among Madagascan *Gulella* having apertural dentition of parietal and palatal teeth and at least one other tooth, *G. microstriata* sp. nov. is unique in its extremely dense rib sculpture.

HOLOTYPE. Station 816 (UF 274937, 1 ad): 12°55'S, 49°03'E: Madagascar: Ankarana Reserve, 100 m. 12-Oct-94.

DRY PARATYPE. Station 816 (UF 274938, 1 juv).

DESCRIPTION OF HOLOTYPE. Height 6.2 mm, diameter 2.7 mm (H/D 2.3), whorls 8.0 (whorls/ln height 4.38). Apical angle 75°, barreling 7.0%. Sutural depth 3.4%, sutural crenulation none. In apertural view, penultimate and body whorls with moderate and extremely dense rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.7, diameter of first 1.5 whorls 1.24 mm, embryonic sculpture of minute riblets. Peristome height 1.7 mm, width 1.7 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.38 mm (0.22 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; a strong baso-columellar lamella; and a very low, broadly rounded baso-columellar tooth. Umbilicus a crevice.

ETYMOLOGY. For the sculpture of small (English "micro-") ridges (Latin "striata").

Gulella kelibea sp. nov.

Fig. 56

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition of parietal and palatal teeth and at least one other tooth, and (b) general rib sculpture weak to none, *G. kelibea* sp. nov. is unique in both its extremely tight coiling (whorls/ln height about 5.4 *vs.* 3.6-5.0) and its lack of evident sutural crenulation.

HOLOTYPE. Station 426 (UF 274863, 1 ad): 23°00'S, 47°44'E: Madagascar: Manombo Reserve, 50 m: rainforest. 23-Jul-95.

DRY PARATYPES. Stations 423 (UF 274871, 1 ad, 3 juv); 424 (UF 274866, 1 ad, 5 juv); 425 (UF 274867, 7 ad, 1 juv); 426 (UF 274868, 3 ad, 1 juv); 427 (UF 274873, 3 ad); 428 (UF 274876, 6 ad); 429 (UF 274875, 1 ad); 430 (UF 274872, 3 ad, 1 juv); 432 (UF 274870, 5 ad); 433 (UF 274865, 1 ad); 434 (UF 274874, 1 ad); 435 (UF 274869, 7 ad, 6 juv; AMS C203586, 1 ad; ANSP 403474, 1 ad; MNHN, 1 ad); 1351 (UF 274864, 1 ad).

ALCOHOL PARATYPES. Stations 427 (UF 275103, 2 ad, 1 juv); 428 (UF 2751052 ad); 429 (UF 275102, 3 ad); 430 (UF 275101, 3 ad); 431 (UF 275100, 11 ad, 4 juv); 432 (UF 275099, 12 ad); 433 (UF 275106, 1 ad, 1 juv); 435 (UF 275104, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 2.8 mm, diameter 1.4 mm (H/D 2.0), whorls 5.5 (whorls/ln height 5.43). Apical angle 95°, barreling -0.9%. Sutural depth 5.3%, sutural crenulation none. In apertural view, penultimate and body whorls with weak rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.68 mm, embryonic sculpture smooth, with faint traces of growth lines. Peristome height 0.9 mm, width 1.0 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.18 mm (0.18 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-rounded palatal tooth (parietal-palatal embayment moderately wide); a small, nubbed columellar recessed baffle; and a moderate, rounded peg-shaped mid-columellar tooth. Umbilicus a minute well.

ETYMOLOGY. For its very (Malagasy "be") small (Malagasy "kely") size, with some word play in Malagasy ("big little").

Gulella bicolor (Hutton, 1834)

Fischer-Piette *et al.* (1994): fig. 50 (specimen)

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition of parietal and palatal teeth and at least one other tooth, and (b) general rib sculpture weak to none, (c) shell height 3.5 mm or greater, and (d) sutural crenulation moderate to strong, *G. bicolor* is unique in having a shell shape steeply pyramidal (*vs.* barreled to columnar), whorls/ln height about 3.6 (*vs.* about 3.7-5.0), and habitat restricted to gardens and settlements.

DESCRIPTION (based on illustration in Fischer-Piette *et al.*, 1994). Height 7.0 mm, diameter 2.0 mm (H/D 3.4), whorls 7.0 (whorls/ln height 3.60). Apical angle 65°, barreling -13.0%. Sutural depth 3.8%, sutural crenulation strong. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes completely, not far below the upper suture. Peristome height 1.9 mm, width 1.8 mm (0.9 shell D; peristome H/W 1.0); apertural lip width 0.40 mm (0.20 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); a large columellar recessed baffle; a moderate baso-columellar lamella; and a large baso-columellar tooth. Umbilicus a crevice.

Gulella analamerae sp. nov.

Fig. 57

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition of parietal and palatal teeth and at least one other tooth and (b) general rib sculpture weak to none, two species are distinguished by their large size due to very loose coiling (whorls/ln height about 3.7-3.8): *G. analamerae* sp. nov. and *G. vohimarae* sp. nov. *G. analamerae* sp. nov. differs from *G. vohimarae* sp. nov. in (a) its narrow (*vs.* broad) baso-columellar tooth, (b) its often present (*vs.* never present) upper-columellar tooth, (c) its tighter coiling (whorls/ln height about 3.8 *vs.* about 3.7), and (d) its smaller initial whorl (diameter of first 1.5 whorls about 1.0-1.1 mm *vs.* about 1.2 mm).

HOLOTYPE. Station 202 (UF 274676, 1 ad): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 310 m: dry deciduous forest. 16-Jul-95.

DRY PARATYPES. Stations 199 (UF 274681, 1 juv); 201 (UF 274684, 30 ad, 11 juv; AMS C203565, 1 ad; ANSP 403475, 1 ad; MNHN, 1 ad); 202 (UF 274678, 1 ad); 203 (UF 274683, 2 ad); 204 (16 ad, 9 juv, specimens lost); 206 (UF 274686, 21 ad, 11 juv); 207 (UF 274682, 1 ad); 208 (UF 274679, 1 juv); 210 (UF 274677, 3 juv); 212 (UF 274685, 4 ad); 213 (UF 274687, 14 ad, 6 juv); 214 (UF 274680, 1 ad, 3 juv).

ALCOHOL PARATYPES. Station 203 (UF 273641, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 9.8 mm, diameter 4.1 mm (H/D 2.4), whorls 8.7 (whorls/ln height 3.81). Apical angle 135°, barreling 7.3%. Sutural depth 4.4%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 1.06 mm, embryonic sculpture smooth. Peristome height 2.8 mm, width 3.0 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.70 mm (0.23 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment narrow); a moderate columellar recessed baffle; a strong baso-columellar lamella; a moderate, peg-like baso-columellar tooth; and a low, very broad mid-columellar tooth. Umbilicus a narrow crevice.

ETYMOLOGY. For Analamera Reserve.

Gulella vohimarae sp. nov.

Fig. 58

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition of parietal and palatal teeth and at least one other tooth and (b) general rib sculpture weak to none, two species are distinguished by their large size due to very loose coiling (whorls/ln height about 3.7-3.8): *G. vohimarae* sp. nov. and *G. analamerae* sp. nov. *G. vohimarae* sp. nov. differs from *G. analamerae* sp. nov. in (a) its broad (*vs.* narrow) baso-columellar tooth, (b) its absent (*vs.* often present) upper-columellar tooth, (c) its looser coiling (whorls/ln height about 3.7 *vs.* about 3.8), and (d) its larger initial whorl (diameter of first 1.5 whorls about 1.2 mm *vs.* about 1.0-1.1 mm).

HOLOTYPE. Station 256 (UF 275053, 1 ad): 13°35'S, 49°59'E: Madagascar: S of Vohimar, 90 m: viny rainforest. 2-Sep-95.

DRY PARATYPES. Stations 256 (UF 275054, 6 ad, 4 juv; AMS C203622, 1 ad; ANSP 403476, 1 ad; MNHN, 1 ad); 257 (UF 275055, 3 ad).

ALCOHOL PARATYPES. Stations 256 (UF 275167, 1 ad); 257 (UF 275166, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 8.1 mm, diameter 3.1 mm (H/D 2.6), whorls 7.7 (whorls/ln height 3.68). Apical angle 95°, barreling 4.8%. Sutural depth 6.2%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.5, diameter of first 1.5 whorls 1.23 mm, embryonic sculpture of very faint growth lines. Peristome height 2.3 mm, width 2.2 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.50 mm (0.23 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment narrow); a large columellar recessed baffle; a strong, recessed baso-columellar lamella; and a large, recessed, broadly rounded baso-columellar tooth that is high in position. Umbilicus imperforate.

ETYMOLOGY. For the city of Vohimar, near the type locality.

Gulella nosybei sp. nov.

Figs. 61, 102

DIAGNOSIS. *G. nosybei* sp. nov. is somewhat similar to the Comoran *G. cryptophora* (Morelet, 1881) but has very much looser coiling. *G. nosybei* sp. nov. is unique among Madagascan *Gulella* in its combination of (a) smooth sculpture; (b) tridentate aperture consisting of parietal, palatal, and mid-columellar teeth and small and inconspicuous recessed columellar baffle; and (c) stout and loosely coiled (whorls/ln height about 4.3, diameter of first 1.5 whorls about 0.9) shell with convex-edged to only slightly concave-edged outer peristome. *G. tendronia* sp. nov. is somewhat similar but much more tightly coiled, with a large columellar recessed baffle and a strongly concave-edged outer peristome. *G. kelibea* sp. nov. is similarly shaped but very much smaller and more tightly coiled, and with a conspicuously nubbed columellar recessed baffle.

HOLOTYPE. Station 118 (UF 274961, 1 ad): 13°25'S, 48°18'E: Madagascar: Lokobe Reserve, Nosy Be, 60 m: rainforest. 25-Jun-95.

FIGURED PARATYPE. Station 546 (UF 274962, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 4.2 mm, diameter 2.0 mm (H/D 2.1), whorls 6.2 (whorls/ln height 4.29). Apical angle 85°, barreling 1.0%. Sutural depth 5.3%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.89 mm, embryonic sculpture smooth. Peristome height 1.2 mm, width 1.2 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.15 mm (0.13 peristome W). Apertural barriers consisting of a large parietal tooth; a large, oblique-butte-shaped palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a large, rounded-triangular mid-columellar tooth. Umbilicus imperforate, apparently.

ETYMOLOGY. For the island of Nosy Be.

Gulella tendronia sp. nov.

Fig. 59

DIAGNOSIS. Only two species of Madagascan *Gulella* have a combination of (a) smooth sculpture; (b) apertural dentition that includes parietal and palatal teeth and a low-positioned mid-columellar tooth; and (c) outer edge of peristome conspicuously concave: *G. tendronia* sp. nov. and *G. celestinae* sp. nov. *G. tendronia* sp. nov. differs from *G. celestinae* sp. nov. in its absence (*vs.* presence) of an upper-columellar tooth and its undivided (*vs.* bifid) parietal and palatal teeth. *G. tendronia* sp. nov. differs from *G. nosybei* sp. nov. in its much tighter coiling, moderate (*vs.* small and inconspicuous) columellar recessed baffle, and strongly concave-edged outer peristome.

HOLOTYPE. Station 201 (UF 274999, 1 ad): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 315 m: dry deciduous forest. 15-Jul-95.

DRY PARATYPE. Station 201 (AMS C203613, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.7 mm, diameter 1.5 mm (H/D 2.5), whorls 6.2 (whorls/ln height 4.70). Apical angle 90°, barreling 2.6%. Sutural depth 5.3%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.78 mm, embryonic sculpture smooth, apparently. Peristome height 1.2 mm, width 1.1 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.13 mm (0.12 peristome W). Apertural barriers consisting of a large parietal tooth; a large, oblique-butte-shaped palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; and a large, rounded-triangular mid-columellar tooth that is low in position. Umbilicus a small crevice.

ETYMOLOGY. For its type locality, a summit (Malagasy "tendrony") within Analamera Reserve.

Gulella celestinae sp. nov.

Fig. 60

DIAGNOSIS. Only two species of Madagascan *Gulella* have a combination of (a) smooth sculpture; (b) apertural dentition that includes parietal and palatal teeth and a low-positioned mid-columellar tooth; and (c) outer edge of peristome conspicuously concave: *G. celestinae* sp. nov. and *G. tendronia* sp. nov. *G. celestinae* sp. nov. differs from *G. tendronia* sp. nov. in its presence (*vs.* absence) of an upper-columellar tooth and its bifid (*vs.* undivided) parietal and palatal teeth. *G. celestinae* sp. nov. is sympatric with the morphologically similar *G. vakinifia* sp. nov., from which it differs in its smooth (*vs.* strongly ribbed) sculpture and its presence (*vs.* absence) of an upper-columellar tooth.

HOLOTYPE. Station 74 (UF 274818, 1 ad): 16°23'S, 45°20'E: Madagascar: Namoroka Reserve, 100 m: dry deciduous forest. 28-May-95.

DRY PARATYPES. Station 74 (UF 274819, 22 ad, 7 juv).

DESCRIPTION OF HOLOTYPE. Height 4.4 mm, diameter 1.9 mm (H/D 2.4), whorls 7.2 (whorls/ln height 4.80). Apical angle 95°, barreling 5.2%. Sutural depth 10.2%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.84 mm, embryonic sculpture smooth. Peristome height 1.3 mm, width 1.2 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.26 mm (0.21 peristome W). Apertural barriers consisting of a large, slightly bifid parietal tooth; a large, bifid palatal tooth (parietal-palatal embayment rather narrow); a moderate columellar recessed baffle; a large, peg-like mid-columellar tooth; and a moderate upper-columellar tooth. Umbilicus a minute crevice.

VARIATION. See Table 2.

ETYMOLOGY. For Celestine Ruth Emberton, daughter of the author, who was near the type locality when she was five months old.

Gulella bemoka sp. nov.

Fig. 62

DIAGNOSIS. Only two species of Madagascan *Gulella* have a combination of (a) smooth sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; and (c) palatal and columellar sides of the peristome straight, parallel, and slanted conspicuously toward the umbilicus: *G. bemoka* sp. nov. and *G. vavakelia* sp. nov. *G. bemoka* sp. nov. differs from *G. vavakelia* sp. nov. in having its palatal tooth notched to receive the parietal tooth and inwardly slanting downward.

HOLOTYPE. Station 241 (UF 274801, 1 ad): 12°00'S, 49°17'E: Madagascar: Cap d'Ambre, near Ambatojanahary, 15 m: dry deciduous forest. 25-Jul-95.

DESCRIPTION OF HOLOTYPE. Height 5.6 mm, diameter 2.1 mm (H/D 2.6), whorls 7.7 (whorls/ln height 4.49). Apical angle 105°, barreling 5.9%. Sutural depth 5.8%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.88 mm, embryonic sculpture smooth. Peristome height 1.7 mm, width 1.5 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.31 mm (0.21 peristome W). Apertural barriers consisting of a moderate parietal tooth; a very large palatal tooth, notched opposite the parietal tooth (parietal-palatal embayment narrow, nearly enclosed); a large columellar recessed baffle; a moderate baso-columellar lamella; and a moderate baso-columellar tooth. Umbilicus imperforate.

ETYMOLOGY. Both for the many mosquitoes at the type locality (Malagasy "be" = many, "moka" = mosquitoes) and for the villagers of Bemoka who helped collect there.

Gulella vavakelia sp. nov.

Fig. 63

DIAGNOSIS. Only two species of Madagascan *Gulella* have a combination of (a) smooth sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; and (c) palatal and columellar sides of the peristome straight, parallel, and slanted conspicuously toward the umbilicus: *G. vavakelia* sp. nov. and *G. bemoka* sp. nov. *G. vavakelia* sp. nov. differs from *G. bemoka* sp. nov. in its unnotched palatal tooth that does not inwardly slant downward.

HOLOTYPE. Station 199 (UF 275004, 1 ad): 12°43'S, 49°28'E: Madagascar: Analamera Reserve, 35 m: dry deciduous forest. 15-Jul-95.

DRY PARATYPES. Stations 199 (UF 275005, 16 ad, 5 juv; AMS C203621, 3 ad; ANSP 403477, 3 ad; MNHN, 3 ad); 201 (UF 275006, 7 ad); 208 (UF 275007, 1 ad).

ALCOHOL PARATYPES. Stations 199 (UF 275164, 3 ad) 201 (UF 275165, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.8 mm, diameter 2.1 mm (H/D 2.7), whorls 7.8 (whorls/ln height 4.43). Apical angle 90°, barreling 4.4%. Sutural depth 5.7%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.85 mm, embryonic sculpture smooth. Peristome height 1.5 mm, width 1.4 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.28 mm (0.20 peristome W). Apertural barriers consisting of a large parietal tooth; a very large, acutely triangular palatal tooth (parietal-palatal embayment fairly narrow, nearly enclosed); a large columellar recessed baffle; a strong, recessed baso-columellar lamella; and a moderate, recessed baso-columellar tooth that is high in position. Umbilicus a very tiny crevice.

ETYMOLOGY. For the small aperture (Malagasy "vava" = mouth, "kely" = small).

Gulella mitsikia sp. nov.

Fig. 64

DIAGNOSIS. Among Madagascan *Gulella* having (a) smooth sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; and (c) palatal and columellar sides of the peristome curved, non-parallel, and not slanted conspicuously inward, *G. mitsikia* sp. nov. is unique in having (a) its baso-columellar tooth large and buttressed more strongly above than below, and (b) its palatal tooth slightly bifid.

HOLOTYPE. Station 579 (UF 274945, 1 ad): 12°58'S, 49°06'E: Madagascar: Ankarana Reserve, 100 m: dry deciduous forest. 25-Aug-95.

DRY PARATYPES. Stations 577 (UF 274947, 10 ad, 11 juv); 579 (UF 274948, 5 ad, 2 juv); 580 (UF 274946, 23 ad, 17 juv; AMS C203600, 3 ad; ANSP 403478, 3 ad; MNHN, 3 ad).

ALCOHOL PARATYPES. Stations 577 (UF 273652, 1 ad); 580 (UF 273653, 2 ad).

DESCRIPTION OF HOLOTYPE (apex broken during measurement). Height 3.6 mm, diameter 1.6 mm (H/D 2.2), whorls estimated at 6.2 (whorls/ln height 4.88). Apical angle 90°, barreling 3.8%. Sutural depth 2.7%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.83 mm, embryonic sculpture smooth. Peristome height 1.1 mm, width 1.0 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.12 mm (0.12 peristome W). Apertural barriers consisting of a large, very slightly bifid parietal tooth; a large, slightly notched palatal tooth (parietal-palatal embayment fairly wide); a moderate columellar recessed baffle; a strong baso-columellar lamella; and a large baso-columellar tooth. Umbilicus a narrow well.

ETYMOLOGY. "To smile" (Malagasy "mitsiky"), for the appearance of the small and toothy aperture.

Gulella bobaombiae sp. nov.

Figs. 65, 66, 67

DIAGNOSIS. Among Madagascan *Gulella* having (a) smooth sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; and (c) baso-columellar tooth buttressed equally above and below, *G. bobaombiae* sp. nov. is unique in its small and tightly coiled shell (whorls/ln height 4.9-5.1, diameter of first 1.5 whorls 0.7-0.8 mm).

HOLOTYPE. Station 401 (UF 274803, 1 ad): 12°11'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 205 m: dry deciduous-baobab forest. 24-Aug-95.

FIGURED PARATYPES. Stations 222 (UF 274804, 1 ad); 229 (UF 274805, 1 ad).

OTHER DRY PARATYPES. Stations 222 (UF 274807, 1 ad); 229 (UF 274808, 3 ad, 1 juv); 401 (UF 274806, 5 ad, 1 juv; AMS C203572, 1 ad; ANSP 403479, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 4.2 mm, diameter 1.7 mm (H/D 2.5), whorls 7.1 (whorls/ln height 4.91). Apical angle 115°, barreling 3.6%. Sutural depth 5.7%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.2, diameter of first 1.5 whorls 0.74 mm, embryonic sculpture smooth, with a trace of growth lines. Peristome height 1.3 mm, width 1.2 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.24 mm (0.19 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; a moderate baso-columellar lamella; and a moderate, knob-like baso-columellar tooth. Umbilicus a minute crevice.

VARIATION. See Table 3.

ETYMOLOGY. For the Butte Bobaomby, sole known locality, and for Cap d'Ambre (Malagasy name Tanjona Bobaomby).

Gulella ambanikelia sp. nov.

Figs. 68, 103

DIAGNOSIS. Among Madagascan *Gulella* having (a) smooth penultimate-whorl sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; (c) baso-columellar tooth buttressed equally above and below; (d) whorls/ln height 4.0-4.4; and (e) diameter of first 1.5 whorls 0.9-1.0 mm, *G. ambanikelia* sp. nov is unique both in the ribbed sculpture of its upper whorls, and in the knobbed shape of its baso-columellar tooth.

HOLOTYPE. Station 805 (UF 274654, 1 ad): 13°01'S, 49°00'E: Madagascar: Ankarana Reserve, 50 m. 8-Oct-94.

FIGURED PARATYPE. Station 805 (UF 274655, 1 ad).

OTHER DRY PARATYPES. Stations 803 (UF 274656, 1 ad); 805 (UF 274657, 50 ad, 3 juv; AMS C203563, 1 ad; ANSP 403480, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.6 mm, diameter 2.3 mm (H/D 2.5), whorls 7.5 (whorls/ln height 4.37). Apical angle 120°, barreling 4.2%. Sutural depth 4.2%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.88 mm, embryonic sculpture of extremely faint growth lines. Peristome height 1.4 mm, width 1.6 mm (0.7 shell D; peristome H/W 0.8); apertural lip width 0.36 mm (0.22 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment narrow); a moderate columellar recessed baffle; a moderate baso-columellar lamella; and a moderate, recessed baso-columellar tooth. Umbilicus imperforate.

VARIATION. Fig. 103 shows a neoadult with only partially formed apertural barriers and lip.

ETYMOLOGY. For the small (Malagasy "kely") tooth on the basal area (Malagasy "ambany") of the aperture.

Gulella ambalaniranae sp. nov.

Figs. 71, 72, 73, 74

DIAGNOSIS. *G. ambalaniranae* sp. nov. is unique among Madagascan *Gulella* in its combination of (a) strong rib sculpture that diminishes completely above the lower suture, and (b) apertural dentition consisting of undivided parietal, palatal, and baso-columellar teeth.

HOLOTYPE. Station 267 (UF 276304, 1 ad): 13°50'S, 49°59'E: Madagascar: Ambalanirana Mountain, 315 m: rainforest. 5-Sep-95.

FIGURED PARATYPES. Station 712 (UF 274631, 3 ad).

OTHER DRY PARATYPES. Stations 258 (UF 274637, 2 ad, 2 juv); 259 (UF 274639, 1 ad); 260 (UF 274634, 1 juv); 261 (UF 274640, 5 ad, 1 juv); 262 (UF 274644, 13 ad, 7 juv); 263 (UF 274632, 1 juv); 264 (UF 274633, 1 ad); 265 (UF 274643, 5 ad, 1 juv); 266 (UF 274641, 2 ad); 267 (UF 274642, 6 ad, 7 juv); 711 (UF 274636, 1 ad); 712 (UF 274635, 85 ad, 19 juv; AMS C203562, 3 ad; ANSP 403481, 3 ad; MNHN, 3 ad); 714 (UF 274638, 2 ad).

ALCOHOL PARATYPES. Stations 258 (UF 273638, 2 ad); 260 (UF 273637, 1 ad); 261 (UF 273634, 1 ad); 262 (UF 273632, 11 ad, 2 juv); 265 (UF 273635, 3 ad, 1 juv); 266 (UF 273639, 1 ad); 267 (UF 273633, 8 ad); 270 (UF 273636, 2 juv); 712 (UF 273631, 86 ad, 7 juv); 714 (UF 273640, 3 ad).

DESCRIPTION OF HOLOTYPE. Height 9.8 mm, diameter 3.8 mm (H/D 2.6), whorls 8.8 (whorls/ln height 3.86). Apical angle 95°, barreling 7.9%. Sutural depth 6.3%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.2, diameter of first 1.5 whorls 1.13 mm, embryonic sculpture of very faint growth lines. Peristome height 2.9 mm, width 2.7 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.75 mm (0.28 peristome W). Apertural barriers consisting of a massive parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment narrow); a large columellar recessed baffle; and a moderate baso-columellar tooth. Umbilicus imperforate.

VARIATION. Baso-columellar tooth sometimes absent.

ETYMOLOGY. For Mount Ambalanirana, N of Sambava.

Gulella namorokae sp. nov.

Fig. 75

DIAGNOSIS. *G. namorokae* sp. nov. is unique among Madagascan *Gulella* in its combination of (a) strong rib sculpture that diminishes completely above the lower suture, and (b) apertural dentition consisting of undivided parietal and baso-columellar teeth, and a strongly bifid palatal tooth.

HOLOTYPE. Station 58 (UF 274952, 1 ad): 16°25'S, 45°23'E: Madagascar: Namoroka Reserve, 120 m: dry deciduous forest. 23-May-95.

DRY PARATYPES. Stations 58 (UF 274954, 7 ad, 1 juv); 61 (UF 274955, 11 ad, 6 juv; AMS C203602, 1 ad; ANSP 403482, 1 ad; MNHN, 1 ad); 64 (UF 274953, 1 ad); 69 (UF 274956, 2 ad); 70 (UF 274958, 6 ad); 74 (UF 274957, 3 juv).

ALCOHOL PARATYPES. Stations 61 (UF 275132, 1 ad); 63 (UF 275133, 2 juv).

DESCRIPTION OF HOLOTYPE. Height 4.0 mm, diameter 1.8 mm (H/D 2.3), whorls 6.8 (whorls/ln height 4.91). Apical angle 100°, barreling 8.0%. Sutural depth 6.7%, sutural crenulation strong. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.83 mm, embryonic sculpture smooth. Peristome height 1.2 mm, width 1.1 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.20 mm (0.19 peristome W). Apertural barriers consisting of a large parietal tooth; a very large, conspicuously bifid palatal tooth (parietal-palatal embayment wide); a moderate columellar recessed baffle; and a moderate baso-columellar tooth that is fairly high in position. Umbilicus an extremely minute crevice.

ETYMOLOGY. For Namoroka Reserve.

Gulella mihomehia sp. nov.

Figs. 76, 77, 78

DIAGNOSIS. *G. mihomehia* sp. nov. is somewhat similar to the South African *G. polita* (Melvill and Ponsonby, 1893) but has a mid-columellar instead of an upper-columellar tooth, has its palatal tooth higher in position and more narrowly based, and has very much looser coiling. *G.*

mihomehia sp. nov. is unique among Madagascan *Gulella* in its combination of (a) strong rib sculpture that diminishes completely above the lower suture, and (b) apertural barriers consisting of notched and closely fitting parietal and palatal teeth (the latter massive), a large columellar recessed baffle, and massive and peg-shaped mid-columellar and baso-central teeth (the latter offset toward the columella and unrecessed to deeply recessed). In apertural dentition, *G. mihomehia* sp. nov. is most similar to *G. vakinifia* sp. nov., from which it differs in its much looser coiling (whorls/ln height about 4.2 *vs.* 4.7-5.0) and its diminished (*vs.* undiminished) rib sculpture.

HOLOTYPE. Station 566 (UF 274949, 1 ad): 12°56'S, 49°07'E: Madagascar: Ankarana Reserve, 90 m: dry deciduous forest. 23-Aug-95.

FIGURED PARATYPES. Stations 568 (UF 274951, 1 ad); 580 (UF 274950, 1 ad).

OTHER DRY PARATYPES. Stations 566 (UF 274941, 7 ad); 568 (UF 274943, 1 ad); 580 (UF 274942, 4 ad); 803 (UF 274944, 93 ad, 71 juv; AMS C203599, 70 ad; ANSP 403483, 10 ad; MNHN, 10 ad); 807 (UF 274940, 2 ad); 815 (UF 274939, 1 ad, 3 juv).

DESCRIPTION OF HOLOTYPE. Height 6.0 mm, diameter 2.6 mm (H/D 2.3), whorls 7.5 (whorls/ln height 4.19). Apical angle 90°, barreling 2.4%. Sutural depth 1.3%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.0, diameter of first 1.5 whorls 1.05 mm, embryonic sculpture smooth, with a trace of growth lines. Peristome height 2.1 mm, width 1.7 mm (0.7 shell D; peristome H/W 1.2); apertural lip width 0.28 mm (0.17 peristome W). Apertural barriers consisting of notched and closely fitting parietal and palatal teeth (the latter massive); a large columellar recessed baffle; and massive, peg-shaped mid-columellar and baso-central teeth (the latter offset toward the columella and unrecessed [but deeply recessed in some paratypes]). Umbilicus a crevice.

ETYMOLOGY. "To laugh" (Malagasy "mihomehy"), for the appearance of the toothy aperture.

Gulella manomboae sp. nov.

Fig. 79

DIAGNOSIS. *G. manomboae* sp. nov. is somewhat similar to the East African *G. peculiaris* (E. A. Smith, 1890), but with much looser coiling and differently shaped apertural teeth. *G. manomboae* sp. nov. is unique among Madagascan *Gulella* for its embryonic sculpture of minute riblets and two subsutural spiral grooves. *G. manomboae* sp. nov. shares its undiminished rib sculpture and its apertural dentition of parietal, palatal, and baso-columellar teeth only with *G. michellae* sp. nov., from which it differs in its much smaller and more tightly coiled shell (whorls/ln height 4.6-4.7 *vs.* 4.0, diameter of first 1.5 whorls about 0.75 mm *vs.* about 1.15 mm).

HOLOTYPE. Station 433 (UF 274906, 1 ad): 23°00'S, 47°44'E: Madagascar: Manombo Reserve, 50 m: rainforest. 27-Feb-96.

DRY PARATYPES. Stations 423 (UF 274912, 4 ad); 424 (UF 274914, 6 ad); 425 (UF 274910, 2 juv); 426 (UF 274917, 2 ad); 427 (UF 274911, 4 ad); 428 (UF 274919, 3 ad, 1 juv; AMS C203596, 1 ad; ANSP 403486, 1 ad; MNHN, 1 ad); 429 (UF 274908, 4 ad, 1 juv); 430 (UF 274913, 4 ad, 1 juv); 431 (UF 274909, 3 ad); 432 (UF 274915, 3 ad, 1 juv); 433 (UF 274918, 1 juv); 435 (UF 274916, 1 juv); 1342 (ANSP 403484, 1 ad); 1347 (ANSP 403485, 1 ad, 1 juv).

ALCOHOL PARATYPES. Stations 427 (UF 275121, 4 ad); 428 (UF 275119, 2 ad, 1 juv); 429 (UF 275120, 8 ad); 430 (UF 275117, 3 ad); 431 (UF 275118, 7 ad); 432 (UF 275124, 4 ad); 433 (UF 275122, 4 ad, 1 juv); 434 (UF 275116, 1 ad); 435 (UF 275123, 3 ad); 1342 (ANSP A19194, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.6 mm, diameter 1.8 mm (H/D 2.0), whorls 6.0 (whorls/ln height 4.64). Apical angle 75°, barreling 2.2%. Sutural depth 3.6%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.75 mm, embryonic sculpture of minute riblets and two subsutural spiral groves. Peristome height 1.2 mm, width 1.2 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.22 mm (0.18 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, triangular palatal tooth curving upward to almost meet the parietal tooth (parietal-palatal embayment fairly wide, nearly enclosed); a large columellar recessed baffle; and a moderate, low, broad-triangular baso-columellar tooth. Umbilicus a very narrow well, opening obliquely.

ETYMOLOGY. For Manombo Reserve.

Gulella michellae sp. nov.

Fig. 80

DIAGNOSIS. *G. michellae* sp. nov. shares its undiminished rib sculpture and its apertural dentition of parietal, palatal, and baso-columellar teeth only with *G. manomboae* sp. nov., from which it differs in its much larger and more loosely coiled shell (whorls/ln height 4.0 *vs.* 4.6-4.7, diameter of first 1.5 whorls about 1.15 mm *vs.* about 0.75 mm). *G. michellae* sp. nov. bears some resemblance to *G. marojejyae* sp. nov., with which it is sometimes sympatric but from which it differs in its undiminished (*vs.* diminished) ribbing, its presence (*vs.* absence) of a baso-columellar tooth, and its much tighter coiling (whorls/ln height 4.0 *vs.* 3.3).

HOLOTYPE. Station 649 (UF 274821, 1 ad): 14°29'S, 49°34'E: Madagascar: W Marojejy Reserve, 700 m: rainforest. 28-Sep-95.

DRY PARATYPES. Stations 649 (UF 274823, 6 ad, 4 juv; AMS C203577, 1 ad; ANSP 403487, 1 ad; MNHN, 1 ad); 677 (UF 274822, 2 ad, 1 juv).

ALCOHOL PARATYPES. Station 649 (UF 273665, 4 ad).

DESCRIPTION OF HOLOTYPE. Height 7.0 mm, diameter 3.0 mm (H/D 2.3), whorls 7.7 (whorls/ln height 3.96). Apical angle 110°, barreling 9.3%. Sutural depth 6.1%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.14 mm, embryonic sculpture smooth. Peristome height 2.2 mm, width 1.9 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.47 mm (0.24 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; a strong baso-columellar lamella; and a low, broad-triangular baso-columellar tooth. Umbilicus a minute crevice.

ETYMOLOGY. For Michelle Kintana Emberton, daughter of the author.

Gulella mahagaga sp. nov.

Fig. 81

DIAGNOSIS. Among Madagascan *Gulella, G. mahagaga* sp. nov. is unique in its combination of (a) undiminished rib sculpture, (b) enormous columellar recessed baffle, and (c) apertural dentition consisting of parietal, palatal, mid-columellar, and baso-central teeth.

HOLOTYPE. Station 98 (UF 274895, 1 ad): 14°02'S, 48°47'E: Madagascar: Tsaratanana Reserve, 950 m: rainforest. 14-Jun-95.

DRY PARATYPES. Stations 98 (UF 274899, 6 ad, 2 juv; AMS C203594, 1 ad; ANSP 403488, 1 ad; MNHN, 1 ad); 103 (UF 274896, 1 ad); 110 (UF 274897, 1 ad); 112 (UF 274901, 6 ad, 1 juv); 114 (UF 274898, 1 ad, 2 juv); 502 (UF 274900, 1 juv).

ALCOHOL PARATYPES. Stations 98 (UF 273602, 1 ad); 112 (UF 273599, 5 ad); 114 (UF 273600, 1 ad); 504 (UF 273601, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 8.1 mm, diameter 3.5 mm (H/D 2.3), whorls 7.9 (whorls/ln height 3.78). Apical angle 85°, barreling 4.3%. Sutural depth 5.8%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.2, diameter of first 1.5 whorls 1.34 mm, embryonic sculpture of minute riblets. Peristome height 2.6 mm, width 2.3 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.40 mm (0.17 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment somewhat narrow); a massive columellar recessed baffle; a moderate, low, broad-triangular mid-columellar tooth; and a large, unrecessed baso-central tooth that is offset toward the columella. Umbilicus imperforate.

ETYMOLOGY. For the surprising (Malagasy "mahagaga") appearance of the apertural barriers.

Gulella hafa sp. nov.

Fig. 82

DIAGNOSIS. Among Madagascan *Gulella, G. hafa* sp. nov. is unique in its columellar dentition of basally merged upper-, mid-, and baso-columellar teeth.

HOLOTYPE. Station 593 (UF 274837, 1 ad): 14°26'S, 49°44'E: Madagascar: Marojejy Reserve, 1300 m: rainforest. 14-Sep-95.

DRY PARATYPES. Station 593 (AMS C203582, 1 ad; MNHN, 1 ad).

ALCOHOL PARATYPE. Station 593 (UF 275085, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 4.9 mm, diameter 2.5 mm (H/D 1.9), whorls 6.1 (whorls/ln height 3.85). Apical angle 80°, barreling 6.2%. Sutural depth 3.9%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.9, diameter of first 1.5 whorls 1.19 mm, embryonic sculpture of faint riblets. Peristome height 1.5 mm, width 1.4 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.13 mm (0.09 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment fairly wide); a small columellar recessed baffle; a moderate, wide baso-columellar tooth; a moderate, triangular mid-columellar tooth; and a moderate, wide upper-columellar tooth. All three columellar teeth are merged together at their bases. Umbilicus a very narrow well.

ETYMOLOGY. "Different" (Malagasy "hafa"), because it is so unlike other Madagascan species of *Gulella* in its columellar dentition.

Gulella benjamini Emberton and Pearce, 2000

Figs. 83, 84

DIAGNOSIS. Only three species of Madagascan *Gulella* have undiminished strong-to-moderate rib sculpture and apertural dentition restricted to parietal, palatal, and mid-columellar teeth: *G. benjamini, G. lubeti*, and *G. mahafinaratra* sp. nov. *G. benjamini* differs from the other two in its much smaller and more tightly coiled shell (whorls/ln height 4.8-5.4 vs. 4.0-4.1).

FIGURED SPECIMEN. Station 1419 (UF 274802, 1 ad).

DESCRIPTION OF HOLOTYPE (USNM 860808). Height 3.3 mm, diameter 1.8 mm (H/D 1.9), whorls 5.8 (whorls/ln height 4.81). Apical angle 100°, barreling 3.4%. Sutural depth 5.6%, sutural crenulation weak. In apertural view, penultimate and body whorls with moderate rib sculpture. Embryonic whorls 1.8, diameter of first 1.5 whorls 0.79 mm, embryonic sculpture of minute, faint riblets. Peristome height 1.1 mm, width 1.0 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.18 mm (0.17 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, triangular palatal tooth (parietal-palatal embayment wide); a small columellar recessed baffle; and a moderate mid-columellar tooth. Umbilicus a crevice.

VARIATION. See Tables 3, 4.

Gulella benjamini saintelucensis subsp. nov.

Fig. 85

DIAGNOSIS. Differs from *G. benjamini s.s.* in its much tighter coiling (whorls/ln height 5.4 *vs*. 4.8-4.9) and its coastal-rainforest (*vs*. montane-rainforest) habitat, that is now well separated from the parent species by uninhabitable, exotic savannah.

HOLOTYPE. Station 6 (UF 274990, 1 ad): 24°46'S, 47°09'E: Madagascar: Forêt Ste. Luce, 10 m: coastal rainforest. 29-Jan-95.

DRY PARATYPE. Station 6 (AMS C203571, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.0 mm, diameter 1.4 mm (H/D 2.1), whorls 5.9 (whorls/ln height 5.40). Apical angle 85°, barreling 2.6%. Sutural depth 6.4%, sutural crenulation weak. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.78 mm, embryonic sculpture smooth. Peristome height 0.9 mm, width 0.9 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.18 mm (0.20 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment wide); a small columellar recessed baffle; and a moderate, rounded mid-columellar tooth. Umbilicus a crevice.

ETYMOLOGY. For the coastal Forêt Sainte Luce.

Gulella lubeti Fischer-Piette, Blanc, Blanc and Salvat, 1994

Fischer-Piette *et al.* (1994): fig. 63 (holotype)

DIAGNOSIS. Only three species of Madagascan *Gulella* have undiminished strong-to-moderate rib sculpture and apertural dentition restricted to parietal, palatal, and mid-columellar teeth: *G. lubeti, G. mahafinaratra* sp. nov., and *G. benjamini*. Both *G. lubeti* and *G. mahafinaratra* sp. nov. differ from *G. benjamini* in their much larger and more loosely coiled shells (whorls/ln height 4.0-4.1 *vs*. 4.8-5.4). *G. lubeti* differs from *G. mahafinaratra* sp. nov. in that its columella is slanted conspicuously outward (*vs*. nearly vertical) and in its moderate (*vs*. very large) palatal tooth.

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al*., 1994). Height 5.6 mm, diameter 2.6 mm (H/D 2.1), whorls 7.0 (whorls/ln height 4.06). Apical angle 85°, barreling 2.9%. Sutural depth 2.9%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Peristome height 1.5 mm, width 1.5 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.20 mm (0.11 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, triangular palatal tooth (parietal-palatal embayment wide); a small columellar recessed baffle; a moderate baso-columellar lamella; and a moderate, triangular-rounded mid-columellar tooth.

Gulella mahafinaratra sp. nov.

Figs. 86, 87, 88

DIAGNOSIS. *G. mahafinaratra* sp. nov. is somewhat similar to the Comoran *G. brevicula* (Morelet, 1882) but has much looser coiling. Only three species of Madagascan *Gulella* have undiminished strong-to-moderate rib sculpture and apertural dentition restricted to parietal, palatal, and mid-columellar teeth: *G. mahafinaratra* sp. nov., *G. lubeti*, and *G. benjamini*. Both *G. mahafinaratra* sp. nov. and *G. lubeti* differ from *G. benjamini* in their much larger and more loosely coiled shells (whorls/ln height 4.0-4.1 *vs*. 4.8-5.4). *G. mahafinaratra* sp. nov. differs from *G. lubeti* in that its columella is nearly vertical (*vs*. slanted conspicuously outward) and its palatal tooth is very large (*vs*. moderate).

HOLOTYPE. Station 668 (UF 274886, 1 ad): 14°32'S, 49°42'E: Madagascar: E of Marojejy Reserve, 1500 m: cloudforest with bamboo. 5-Oct-95.

FIGURED PARATYPES. Stations 648 (UF 274888, 1 ad); 661 (UF 274887, 1 ad).

OTHER DRY PARATYPES. Stations 648 (UF 274890, 1 juv); 661 (UF 274891, 2 juv; MNHN, 1 ad); 666 (AMS C203593, 1 ad); 668 (UF 274889, 2 juv); 671 (UF 274894, 1 ad); 674 (UF 274893, 1 juv); 742 (UF 274892, 1 ad).

ALCOHOL PARATYPES. Stations 634 (UF 275108, 1 ad); 648 (UF 275114, 6 ad, 1 juv); 661 (UF 275112, 1 ad); 666 (UF 275110, 5 ad, 1 juv); 668 (UF 275109, 2 ad, 1 juv); 674 (UF 275113, 1 ad); 677 (UF 275115, 1 ad); 742 (UF 275111, 1 ad, 1 juv); 758 (UF 275107, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 7.2 mm, diameter 3.0 mm (H/D 2.4), whorls 8.0 (whorls/ln height 4.05). Apical angle 80°, barreling 5.2%. Sutural depth 5.2%, sutural crenulation weak. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls estimated at 2.0, diameter of first 1.5 whorls 1.14 mm, embryonic sculpture smooth, apparently. Peristome height 2.0 mm, width 1.8 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.44 mm (0.24 peristome W). Apertural barriers consisting of a moderate parietal tooth; a very large, triangular palatal tooth (parietal-palatal embayment fairly wide); a moderate columellar recessed baffle; and a moderate, rounded mid-columellar tooth. Umbilicus an extremely minute crevice.

ETYMOLOGY. For the beautiful (Malagasy "mahafinaratra") shell.

Gulella hafahafa sp. nov.

Figs. 89, 90, 91, 92

DIAGNOSIS. *G. hafahafa* sp. nov. is unique among

Madagascan *Gulella* both for its beaded embryonic sculpture and for its apertural dentition that includes upper-columellar, mid-columellar, and baso-central teeth.

HOLOTYPE. Station 349 (UF 274838, 1 ad): 16°19'S, 49°44'E: Madagascar: W of Sahasoa, S of Mananara, 480 m: hardwood rainforest. 18-Oct-95.

FIGURED PARATYPES. Stations 367 (UF 274839, 1 ad); 1540 (UF 274840, 1 juv); 1545 (UF 274841, 1 juv).

OTHER DRY PARATYPES. Stations 349 (UF 274844, 1 juv); 351 (UF 274845, 1 juv); 353 (UF 274843, 1 ad); 355 (UF 274842, 1 ad); 356 (UF 274847, 1 juv); 357 (UF 274846, 1 juv); 367 (UF 274848, 1 juv; AMS C203583, 1 ad; ANSP 403491, 1 ad; MNHN, 1 ad); 1529 (ANSP 403489, 1 juv); 1549 (ANSP 403490, 1 ad).

ALCOHOL PARATYPES. Stations 349 (UF 275091, 2 ad); 351 (UF 275088, 1 juv); 353 (UF 275089, 2 juv); 356 (UF 275087, 3 ad, 1 juv); 357 (UF 275090, 2 ad); 744 (UF 275086, 2 ad); 1529 (ANSP A19195, 1 juv); 1536 (ANSP A19196, 1 juv); 1540 (ANSP A19197); 1547 (ANSP A19198, 1 juv).

DESCRIPTION OF HOLOTYPE. Height 7.7 mm, diameter 3.4 mm (H/D 2.3), whorls 7.6 (whorls/ln height 3.73). Apical angle 80°, barreling 7.4%. Sutural depth 4.8%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture. Diameter of first 1.5 whorls 1.03 mm. Peristome height 2.8 mm, width 2.2 mm (0.7 shell D; peristome H/W 1.2); apertural lip width 0.75 mm (0.34 peristome W). Apertural barriers consisting of a massive parietal tooth; a massive, slightly bifid palatal tooth (parietal-palatal embayment narrow, nearly enclosed); a small columellar recessed baffle; a moderate, triangular mid-columellar tooth; a peg-like upper-columellar tooth; and a moderate baso-central tooth that is rather deeply recessed and offset toward the columella. Umbilicus a crevice.

DESCRIPTION OF EMBRYONIC SHELL OF PARATYPE UF 274839. Embryonic whorls 2.1, embryonic sculpture first smooth, then beaded (faint riblets interrupted by faint spiral striae).

ETYMOLOGY. For its unusual (Malagasy "hafahafa" = strange) apertural dentition.

VARIATION. See Table 3.

Gulella vatosoa sp. nov.

Fig. 93

DIAGNOSIS. Among Madagascan *Gulella, G. vatosoa* sp. nov. is unique in its strongly ribbed embryonic sculpture. Among species with undiminished strong rib sculpture and with apertural dentition restricted to parietal, palatal, and mid-columellar teeth, it is the only species in which the palatal and mid-columellar teeth point directly toward each other.

HOLOTYPE. Station 313 (UF 275043, 1 ad): 15°33'S, 49°59'E: Madagascar: W Masoala Peninsula, 305 m: hardwood rainforest. 28-Sep-95.

DRY PARATYPES. Stations 279 (UF 275044, 1 juv); 282 (UF 275048, 1 juv); 289 (UF 275045, 1 juv); 303 (UF 275046, 1 ad); 313 (UF 275051, 2 juv); 349 (UF 275052, 1 ad, 1 juv); 351 (UF 275049, 4 juv; ANSP 403492, 1 ad; MNHN, 1 ad); 353 (AMS C203620, 1 ad); 354 (UF 275050, 2 ad); 358 (UF 275047, 1 ad).

ALCOHOL PARATYPES. Stations 283 (UF 275154, 1 ad); 284 (UF 275161, 1 ad); 303 (UF 275157, 1 ad); 307 (UF 275160, 2 juv); 342 (UF 275159, 1 ad); 349 (UF 275155, 1 ad, 1 juv); 351 (UF 275156, 3 ad); 353 (UF 275158, 4 ad); 354 (UF 275162, 1 ad); 357 (UF 275163, 5 ad); 358 (UF 275153, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 4.1 mm, diameter 2.1 mm (H/D 1.9), whorls 6.2 (whorls/ln height 4.41). Apical angle 80°, barreling 4.8%. Sutural depth 7.5%, sutural crenulation weak. In apertural view, penultimate and body whorls with very strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.80 mm, embryonic sculpture of strong riblets. Peristome height 1.4 mm, width 1.2 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.28 mm (0.23 peristome W). Apertural barriers consisting of a large parietal tooth; a large, moderately bifid palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a large, peg-triangular mid-columellar tooth directly opposite the palatal tooth. Umbilicus a narrow well.

ETYMOLOGY. "Gem" (Malagasy "vatosoa"), for the pleasing appearance of the shell.

Gulella vakinifia sp. nov.

Figs. 94, 95, 96, 97

DIAGNOSIS. Among Madagascan species of *Gulella* with undiminished strong rib sculpture, *G. vakinifia* sp. nov. is unique in its apertural dentition of parietal, palatal, low-positioned mid-columellar, and recessed baso-central teeth. In apertural dentition, *G. vakinifia* sp. nov. is most similar to *G. mihomehia* sp. nov., from which it differs in its much tighter coiling (whorls/ln height about 4.7-5.0 *vs.* 4.2) and its undiminished (*vs.* diminished) rib sculpture. *G. vakinifia* sp. nov. is sometimes sympatric with the morphologically similar *G. celestinae* sp. nov., from which it differs in its ribbed (*vs.* smooth) sculpture and its absence (*vs.* presence) of an upper-columellar tooth.

HOLOTYPE. Station 254 (UF 275023, 1 ad): 19°02'S, 44°48'E: Madagascar: Bemaraha Reserve, 150 m: forest along limestone wall. 18-Jun-95.

FIGURED PARATYPES. Stations 62 (UF 275025, 1 ad); 254 (UF 275024, 1 ad); 490 (UF 275026, 1 ad).

OTHER DRY PARATYPES. Stations 61 (UF 275038, 1 ad, 1 juv); 62 (UF 275042, 3 ad, 1 juv); 64 (UF 275028, 4 ad); 65 (UF 275036, 3 ad); 68 (UF 275032, 4 ad); 74 (UF 275035, 30 ad, 1 juv; AMS C203619, 15 ad); 245 (UF 275027, 6 ad); 248 (UF 275041, 1 ad); 249 (UF 275034, 2 ad, 2 juv; AMS C203617, 8 ad, 2 juv); 252 (UF 275039, 1 ad); 254 (UF 275029, 2 ad; AMS C203618, 3 ad; ANSP 403493, 1 ad; MNHN, 1 ad); 489 (UF 275033, 4 ad); 490 (UF 275030, 7 ad, 5 juv); 494 (UF 275031, 6 ad).

ALCOHOL PARATYPES. Stations 64 (UF 275150, 2 ad); 65 (UF 275152, 1 ad); 490 (UF 275151, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 3.5 mm, diameter 1.7 mm (H/D 2.1), whorls 6.3 (whorls/ln height 4.99) Apical angle 85°, barreling 5.7%. Sutural depth 4.8%, sutural crenulation strong. In apertural view, penultimate and body whorls with very strong rib sculpture Embryonic whorls 2.1, diameter of first 1.5 whorls 0.78 mm, embryonic sculpture smooth. Peristome height 1.6 mm, width 1.1 mm (0.6 shell D; peristome H/W 1.4); apertural lip width 0.30 mm (0.28 peristome W). Apertural barriers consisting of a massive, slightly notched parietal tooth; a massive, bifid palatal tooth (parietal-palatal embayment narrow); a moderate columellar recessed baffle; a moderate baso-columellar lamella; a moderate to large, rounded mid-columellar tooth; and a small, recessed baso-central tooth. Umbilicus a crevice.

VARIATION. See Tables 2, 3, 4.

ETYMOLOGY. For the split (Malagasy "vaky") palatal apertural tooth (Malagasy "nify").

Gulella orchida sp. nov.

Figs. 98, 99

DIAGNOSIS. Among Madagascan species of *Gulella* with undiminished strong rib sculpture, only two species have a palatal tooth that (a) is so massive it fills half the aperture and (b) has a notch into which the parietal tooth enters directly, and (c) that have a recessed baso-columellar tooth: *G. orchida* sp. nov. and *G. magnorchida* sp. nov. *G. orchida* sp. nov. differs from *G. magnorchida* sp. nov. in its presence (*vs.* absence) of an upper-columellar tooth, and in its tighter coiling (whorls/ln height 4.4-4.5 *vs.* 4.2-4.3).

HOLOTYPE. Station 218 (UF 274965, 1 ad): 12°23'S, 49°19'E: Madagascar: Montagne des Orchides, 385 m: dry deciduous forest. 20-Jul-95.

FIGURED PARATYPE. Station 221 (UF 274966, 1 ad).

OTHER DRY PARATYPES. Stations 215 (UF 274969, 6 ad, 1 juv); 217 (UF 274968, 18 ad, 2 juv); 218 (UF 274970, 17 ad, 8 juv); 221 (UF 274967, 30 ad, 6 juv; AMS C203604, 3 ad; ANSP 403494, 3 ad; MNHN, 3 ad).

ALCOHOL PARATYPES. Stations 215 (UF 275136, 3 ad); 218 (UF 275134, 3 ad); 221 (UF 275135, 5 ad).

DESCRIPTION OF HOLOTYPE. Height 5.8 mm, diameter 2.3 mm (H/D 2.5), whorls 7.5 (whorls/ln height 4.26). Apical angle 100°, barreling 5.4%. Sutural depth 5.4%, sutural crenulation strong. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes little between upper and lower sutures. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.89 mm, embryonic sculpture smooth. Peristome height 1.9 mm, width 1.5 mm (0.6 shell D; peristome H/W 1.3); apertural lip width 0.38 mm (0.25 peristome W). Apertural barriers consisting of a large parietal tooth, a massive, deeply notched palatal tooth, into which the parietal tooth enters (parietal-palatal embayment narrow, nearly enclosed); a large columellar recessed baffle; a strong baso-columellar lamella; a moderate baso-columellar tooth; and a large, low, rounded, mid-columellar tooth in a high position. Umbilicus imperforate.

ETYMOLOGY. Both for Montagne des Orchides and for the complex dentition reminiscent of orchid petals.

Gulella magnorchida sp. nov.

Fig. 100

DIAGNOSIS. Among Madagascan species of *Gulella* with undiminished strong rib sculpture, only two species have a palatal tooth that (a) is so massive it fills half the aperture and (b) has a notch into which the parietal tooth enters directly, and (c) that have a recessed baso-columellar tooth: *G. magnorchida* sp. nov. and *G. orchida* sp. nov. *G. magnorchida* sp. nov. differs from *G. orchida* sp. nov. in its absence (*vs.* presence) of an upper-columellar tooth, and in its looser coiling (whorls/ln height 4.2-4.3 *vs.* 4.4-4.5).

HOLOTYPE. Station 401 (UF 274881, 1 ad): 12°11'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 205 m: dry deciduous-baobab forest. 24-Aug-95.

DRY PARATYPES. Stations 400 (UF 274883, 2 ad); 401 (UF 274884, 19 ad, 4 juv; AMS C203592, 1 ad; ANSP 403495, 1 ad; MNHN, 1 ad); 403 (UF 274882, 2 ad, 3 juv); 405 (UF 274885, 3 ad, 3 juv).

DESCRIPTION OF HOLOTYPE. Height 8.3 mm, diameter 2.8 mm (H/D 3.0), whorls 9.4 (whorls/ln height 4.43). Apical angle 105°, barreling 6.8%. Sutural depth 3.4%, sutural crenulation strong. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.2, diameter of first 1.5 whorls 1.04 mm, embryonic sculpture smooth, with traces of miniscule riblets. Peristome height 2.3 mm, width 2.0 mm (0.7 shell D; peristome H/W 1.2); apertural lip width 0.47 mm (0.24 peristome W). Apertural barriers consisting of a large parietal tooth; a massive, broad palatal tooth notched to receive the parietal tooth (parietal-palatal embayment fairly narrow, nearly enclosed); a large columellar recessed baffle; a moderate baso-columellar lamella; and a moderate, rounded-peg-shaped baso-columellar tooth. Umbilicus imperforate.

ETYMOLOGY. For its resemblance to *Gulella orchida* sp. nov. and its diagnostically large (Latin "magn-") embryonic whorls.

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Behavioral responses of glochidia of freshwater mussels (Bivalvia: Unionidae) to chemical cues of fish

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Abstract: Glochidia of wavyrayed lampmussels, *Lampsilis fasciola* Rafinesque, 1820 and rainbow mussels, *Villosa iris* (Lea, 1829) were exposed to mucus, blood, blood by-products, and amino acids of host smallmouth bass, *Micropterus dolomieu* Lacepède, 1802 and non-host carp, *Cyprinus carpio* Linnaeus, 1758 to measure their chemosensory responses. A valve closure index (VCI), the product of percentage of glochidia closed 1 min after exposure times the reciprocal of the time (sec) to closure of the first glochidium upon exposure, was developed and used as the response variable. The median VCI of carp mucus exposures was significantly greater than that of bass mucus for *V. iris* ($p < 0.04$) and for L. fasciola ($p < 0.04$). We believe that this result was due to blood in the carp mucus samples. Glochidia of *V. iris* also were exposed to carp blood, carp serum, carp plasma, amino acids, and fibrinogen. The VCI values for carp serum treatments were significantly less than those of carp blood ($p < 0.04$). The VCI values for carp serum treatments were significantly less than those for carp plasma ($p < 0.04$). These results indicate that fibrinogen may be a principle response cue for glochidia. From lowest to highest VCI values, statistically significant ($p = 0.05$) treatment groupings included: water and heparin; L-threonine/L-serine and L-alanine/L-proline; carp serum, saline, thrombin, and bass mucus; carp mucus, blood, and plasma; and a fibrinogen/thrombin mixture, and fibrinogen alone. VCI values were highest in fibrinogen treatment exposures, indicating that glochidia may respond initially to chemicals involved in the encystment process, rather than to host fish status or nutrients required for metamorphosis.

Key Words: Freshwater mussels, Unionidae, chemosensory, host fish, valve closure index.

The ability to detect and respond to chemical stimuli emanating from fish hosts has been demonstrated in glochidia. Heard and Hendrix (1964) reported that glochidial valve closure in three species of Lampsilinae was affected by the blood of many fish species and various amino acids. They hypothesized that amino acids in fish blood stimulated valve closure of glochidia. Lukacosovics and Labos (1965) determined that fish serum and mucus increased the likelihood of valve closure in the swan mussel, *Anodonta cygnea* (Linnaeus, 1758). Young and Williams (1984) observed that the opening and closing of valves greatly increased when glochidia of the eastern pearlshell, *Margaritifera margaritifera* (Linnaeus, 1758), were exposed to host mucus, blood, and gill and fin tissue of brown trout, *Salmo trutta* Linnaeus, 1758.

Wood (1974) investigated glochidial response to fish hosts and determined that increased valve-snapping behavior in glochidia of *A. cygnea* is related to the detection of "substances found in the mucus and epidermal layers of fish." She also reported that sustained valve closure in glochidia was dependent on chemical cues. Mantle cell sensory hairs were determined to contain the responsive chemoreceptors. Wood (1974) isolated amino acids from fish mucus, exposed glochidia to them, and found that these substances were not important for behavioral response. She described the closure responses of glochidia as occurring in two phases, initial and delayed. Two small molecules, identified in fish mucus, were responsible for these valve closure phases. The first was an uncharged molecule, and was termed an "initial response substance." The second was a positively charged "delayed response substance." These unidentified molecules were responsible for initial and delayed valve closure, respectively.

The purpose of this study was to investigate valve closure behavior of glochidia of wavyrayed lampmussels, *Lampsilis fasciola* Rafinesque, 1820 and rainbow mussels, *Villosa iris* (Lea, 1829) in response to mucus and amino acids of smallmouth bass, *Micropterus dolomieu* Lacepède, 1802, which are hosts, and carp, *Cyprinus carpio* Linnaeus, 1758, which are not hosts (Henley, 1996). Because a higher

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percentage of glochidia elicited valve closing behavior when exposed to non-host mucus, additional experiments were conducted using *C. carpio* blood and blood components.

MATERIALS AND METHODS

The abilities of glochidia of *Villosa iris* and *Lampsilis fasciola* to respond to host (*Micropterus dolomieu*) and non-host (*Cyprinus carpio*) mucus, blood, blood components, and amino acids were tested. Blood was drawn from the fish using an 18-gauge needle and syringe. In an exploratory test to determine whether blood of anesthetized fish stimulated different behavioral responses in glochidia, a subsample of the total number of carp sampled was anesthetized using tricaine methanesulfonate (Finquel[2], Argent Chemical Laboratories, Redmond, Washington). Mucus was scraped from fish, frozen at -60 °C, and thawed for experimental use. Unless otherwise noted, all commercially purchased chemical compounds and test kits were obtained from Sigma Chemical Co.[2], St. Louis, Missouri. Mucus was analyzed for total protein, as well as total and free amino acid content. Total protein content (mg/l) was measured using a Bicinchoninic Acid Protein Assay Kit[2]. Chromatographic analysis of total and free amino acids was conducted using a Pico-Tag Amino Acid Analysis System[2] (Millipore Corp., Bedford, Massachusetts). Glochidia were extracted from *V. iris* and *L. fasciola* by gill irrigation using a 26-gauge needle and syringe, and tested for viability using a weak saline solution (Bruenderman and Neves, 1993). Components of blood from carp were separated using 10 ml Vacutainer Evacuated Blood Collection Tubes[2] (Becton Dickinson, Rutherford, New Jersey) containing 143 USP Units of sodium heparin.

Glochidia from 3 females with 5 replicates per female were placed in separate petri dishes. Thus, the sample size was 3 per treatment, and a replicate consisted of 2 drops of distilled water containing 30 to 168 glochidia placed in a petri dish. These replicates of glochidia were exposed to 2 drops of test solution (described below) from a 26-gauge needle and syringe. Time (sec) was recorded to first valve closure after solution introduction, as was the percentage of glochidial valves closed after 1 min. A multiplicative valve closure index (VCI) for each replicate was developed and calculated by multiplying the reciprocal of time to first valve closure by the percentage (decimal) of glochidia closed after 1 min. The rationale for this method was that a higher percentage of valve closure and greater speed to first closure should be related to the sensitivity of glochidia to test substances. The reciprocal of time to first closure was calculated and used in the VCI formula, so that greater weighting could be applied to VCI values in experiments with faster initial response times.

Glochidia of *Villosa iris* and *Lampsilis fasciola* were first exposed to host and non-host mucus. Because VCI values were higher for glochidia subjected to carp mucus (non-host) than to bass mucus (host), glochidia of *V. iris* were tested against carp blood, blood components, amino acids, and sheep fibrinogen (Table 1). These tests were conducted because of suspected blood in carp mucus samples; *i.e.*, mucus scraping often caused surface epidermal bleeding in the carp. Sparse data were available on the amino acid composition of fish mucus, and none was found for the fish species used in this experiment. The mixtures of amino acids used in experiments were L-alanine/L-proline and L-threonine/L-serine based on an analysis of gill mucin of rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792) by Lumsden and Ferguson (1994). Since fish fibrinogen was not available commercially, sheep fibrinogen was used. This substitute was selected since fibrinogen is similar among vertebrate taxa (Doolittle, 1990). Fibrinogen is important in the blood clotting process through the thrombin-catalyzed conversion of fibrinogen to fibrin (Doolittle, 1990). A fibrinogen/thrombin mixture also was tested to determine whether VCI responses to fibrin differed significantly from those of fibrinogen. The thrombin used in this mixture also was from sheep, as previously described. With these substances, an attempt was made to determine whether a primary chemical cue was responsible for differences in VCI ratings.

Results of test groups were compared nonparametrically using the Kruskal-Wallis test for differences among group medians, and the Multiple Comparisons Test for differences among level medians in the MOOD command in Minitab 10.5[2] (Minitab Inc., State College, Pennsylvania). Individual nonparametric comparisons were conducted using the Mann-Whitney test for differences among group medians.

RESULTS AND DISCUSSION

The Kruskal-Wallis test detected differences among treatment medians ($p < 0.0001$); therefore, nonparametric multiple comparisons were protected at this alpha level. The range of VCI medians for all treatments was from 0.0 for water and heparin to 209.0 for fibrinogen (Table 1). The components of the VCI; namely, the reciprocal of the time (sec) to first valve closure in treatment replicates, and the percentage of glochidial valves closed in replicates after 1 min, were not related to the number of glochidia used in treatment replicates ($r^2 = 0.02$, $p = 0.06$ and $r^2 = 0.00$, $p = 0.73$, respectively). The reciprocal of the time to first valve

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[2] Use does not imply endorsement by the U. S. government.

Table 1. Median Valve Closure Index (VCI) values for *Lampilis fasciola* and *Villosa iris* and concentrations of treatment substances used. Multiple comparisons are for exposures with *V. iris*; family error rate = 0.05. Treatments with the same letter are not significantly different. ND = not determined.

		Species		
Substance	Concentration Analysis	*L. fasciola*	*V. iris*	Multiple Comparison Analysis
distilled water	ND	0.0	0.0	a
sodium heparin	143 USP units		0.0	a
L-threonine / L-serine	threonine=10.0% and L-serine=8.0%		1.0	b
L-alanine / L-proline	alanine=17.6% and proline=9.9%		5.7	b
carp serum	ND		10.1	c
thrombin	144 NIH units		13.6	c
saline	0.85%		20.4	c
bass mucus	1.24 mg protein/ml	23.8	43.7	c
carp mucus	0.907 mg protein/ml	50.1	74.6	d
carp blood without Finquel[3]	ND		75.1	d
carp plasma	ND		89.3	d
fibrinogen / thrombin	thrombin=144 NIH units and fibrinogen = 1.0%		174.9	e
fibrinogen	1.0%		209.0	e

closure component of the VCI was most predictive of calculated VCI values ($r^2 = 0.88$, $p < 0.0001$).

Surprisingly, VCI values for both *Villosa iris* and *Lampsilis fasciola* glochidia were higher with exposure to non-host (carp) mucus than to host (bass) mucus. For *V. iris*, the VCI of carp mucus exposures was significantly greater than that of bass mucus ($p < 0.04$), as was the similar comparison for *L. fasciola* ($p < 0.04$). We believe that this result was due to blood in the carp mucus samples. The carp mucus was pink, but we saw no evidence of blood in the bass mucus. Also, there were differences in VCI values between the glochidia of both mussel species within similar mucus types. The VCI values of *V. iris* were significantly higher with exposure to bass mucus than VCI values of *L. fasciola* ($p < 0.04$), and VCI values of *V. iris* were significantly greater than those of *L. fasciola* in carp mucus exposures ($p < 0.04$) (Table 1). These findings reaffirm that glochidia possess chemosensory abilities. Despite this result, it was surprising that the VCI values of these glochidia were higher with exposure to carp (non-host) mucus than to bass (host) mucus. These results infer that the responses of glochidia may not relate to host/non-host status of the fish from which mucus-based cues originate.

The total protein content in bass mucus and carp mucus was 1.24 mg/l and 0.91 mg/l, respectively. Total (hydrolyzed) amino acid composition of the two types of mucus was very similar (Table 2). The only substantive differences between total (hydrolyzed) amino acids found in bass mucus and carp mucus were that bass mucus included B-aminoisobutyric acid, whereas carp mucus did not; and carp mucus included hydroxyproline, whereas bass mucus did not. A comparison of free amino acids (mg/l) contained in bass mucus and carp mucus samples shows differences in occurrence and concentrations (Table 2). There were five free amino acids in carp mucus that were missing in bass mucus; hydroxyproline, anserine nitrate, histidine, methionine sulfone, and arginine. Most free amino acid concentrations were much greater in carp mucus than in bass mucus (Table 2). Identification of amino acid(s) possibly responsible for an increase or decrease in VCI values is difficult because the concentration of an amino acid may not be reflective of its effectiveness as a chemical cue. A free amino acid may be in low concentration but readily soluble; therefore, it may be a more potent chemical cue than an amino acid in greater concentration but relatively insoluble.

Because VCI values were significantly greater in carp mucus than in bass mucus exposures, and because we suspected that blood was present in the carp mucus samples, glochidia of *Villosa iris* were tested with carp blood and blood components. For comparison, we also tested glochidia of this mussel species for responses to various amino acids (Table 1). When testing the constituent components of carp blood, we found that the VCI values associated with blood-based tests were ordered and significantly different. The VCI values for tests using carp serum (lacking clotting factors such as fibrinogen) were significantly less than those for carp blood ($p < 0.04$), but VCI values for carp blood tests were not significantly less than those for carp plasma (both of which contain clotting factors) ($p < 0.19$). The VCI values for carp serum tests were significantly less than those for carp plasma ($p < 0.04$). Noteworthy is that the VCI values for fibrinogen exposures were the highest of all tested substances (Table 1). The VCI values for thrombin/fibrinogen exposures were not significantly different from those for fibrinogen ($p = 1.0$), substantiating the hypothesis that the higher VCI medians associated with fibrinogen were due to chemical stimulation, rather than tactile stimulation from fibrin. VCI values associated with blood exposures from anesthetized versus unanesthetized carp did not differ significantly ($p = 1.0$).

Table 2. Mean concentrations (mg/l) of free and hydrolyzed amino acids in carp (*Cyprinus carpio*) and bass (*Micropterus dolomieu*) mucins.

	Free Amino Acids (mg/l)		Hydrolyzed Amino Acids (mg/l)	
Amino Acid	Bass	Carp	Bass	Carp
phosphoserine	0.00	0.00	0.00	0.00
aspartic acid	3.34	5.32	78.52	83.06
glutamic acid	7.69	25.35	146.52	143.53
α-aminoadipic acid	0.00	0.00	0.00	0.00
hydroxyproline	0.00	1.56	0.00	1.07
phosphoethanolamine	3.14	2.12	1.78	1.03
serine	5.39	13.06	74.99	79.92
asparagine	0.00	6.61	0.00	0.00
glycine	3.90	7.44	62.85	67.47
glutamine	1.98	7.17	0.00	0.00
B-alanine	0.00	0.00	0.00	0.00
taurine	38.72	51.74	33.56	46.76
histidine	0.00	3.52	23.65	24.43
γ-aminobutyric acid	0.00	0.00	0.00	0.00
citrulline	0.00	0.00	0.00	0.00
threonine	5.12	10.15	55.58	51.48
alanine	5.91	14.32	62.16	65.99
B-aminoisobutyric acid	1.27	0.49	1.57	0.00
carnosine	0.00	0.00	0.00	0.00
arginine	0.00	23.42	54.87	56.31
proline	1.74	6.73	44.83	54.46
1-methylhistidine	0.00	0.00	0.00	0.00
anserine nitrate	0.00	0.00	0.00	0.00
3-methylhistidine	0.00	0.00	0.00	0.00
ethanolamine	1.66	2.49	3.55	3.34
α-amino-n-butyric acid	0.00	0.00	0.00	0.00
tyrosine	3.01	14.08	38.97	34.19
valine	2.33	12.46	45.60	47.44
methionine	0.00	5.70	27.96	29.83
cystathionine	0.00	0.00	0.00	0.00
cystine	0.00	0.00	0.00	0.00
cysteine	0.00	0.00	8.80	7.31
isoleucine	1.41	9.87	33.63	34.96
leucine	3.03	20.57	87.13	88.31
hydroxylysine 1	0.00	0.00	0.00	0.00
hydroxylysine 2	0.00	0.00	0.00	0.00
phenylalanine	2.40	14.59	46.64	50.09
tryptophan	0.28	3.35	0.00	0.00
ornithine	1.37	0.89	1.99	1.24
lysine	2.93	28.45	90.78	96.24

Further analysis of test results, using multiple comparisons of treatment VCI values, revealed that there were 5 distinct and significantly different substance groupings (Table 1). From lowest to highest response, treatment groupings of VCI medians included: water and heparin; L-threonine/L-serine and L-alanine/L-proline; carp serum, saline, thrombin, and bass mucus; carp mucus, carp blood, and carp plasma; and fibrinogen/thrombin and fibrinogen (Table 1). From this analysis, it was apparent that VCI values increased with an increase in the concentration of fibrinogen. Test results showed that the VCI values for the amino acid group were among the lowest measured, with VCI scores slightly greater than water and heparin (Table 1). This is a clarification of the work of Heard and Hendrix (1964) and Wood (1974); *i.e.* although amino acids can induce valve closure response in glochidia, they are seemingly marginal cues. In fact, glochidia were observed in pre-testing experiments to respond to substances unrelated to the encystment process, including heparin and human saliva (VCI ranges were 0.0 to 0.99 and 33.4 to 110.5, respectively). In this context, the VCI provides a refinement on methods previously used in chemosensory experiments with glochidia because it uses group, as well as individual, responses. Thus, the VCI allows measurement of the strength of responses to various treatments, rather than simply answering a yes or no question concerning the chemosensory responses of glochidia.

It may be appropriate to partition chemical cues into strength-of-response categories. Minor chemical cues may be those that induce marginal valve closing responses from glochidia, whereas principle cues may be those that most readily initiate responses. This is to say that a minor cue may one to which a smaller percentage of glochidia elicit valve closing behavior with a slower initial closing time, and vice-versa for principal cues. Substances such as heparin, thrombin, fish mucus, aqueous forms of amino acids, and blood plasma are seemingly minor chemical cues, while fibrinogen seems to be a principle cue. This is not to say that amino acids are not included in the chemical structure of fibrinogen; indeed, it may be that binding sites, such as the Gly-Pro-Arg-ending peptides on the fibrinogen molecule are principle chemical cues for glochidia (Doolittle, 1990). The level of tissue damage that occurs when glochidia attach to fish is undescribed, but some must occur, especially with the attachment of hooked glochidia. Because fibrinogen is vital in the process of fluid retention after injury (Van Vliet *et al.*, 1985; Doolittle, 1990) and, therefore, in the encystment process, the glochidial response to fibrinogen is seemingly appropriate because glochidia may have an inherent biochemical recognition system that is based on fibrinogen or similar substances. Fibrinogen also plays a vital role in masking bacteria from host immune assault (Whitnack and Beachey, 1982; Whitnack *et al.*, 1984; Horstmann *et al.*, 1992). In several types of streptococci, fibrinogen binds to M protein in surface fabrillae and prevents the binding of complement (C3) to the streptococcal cell surface. Thus, fibrinogen impedes access of complement proteins to cell wall receptors (Whitnack and Beachey, 1982). In this way, streptococci are masked from phagocytosis. Because clotting factors may be involved in the encystment process, the strong behavioral response of glochidia to fibrin and fibrinogen could be related to these important biochemical processes.

The process of the thrombin-catalyzed conversion of fibrinogen to fibrin has apparently been in place for 450 million years in primitive fishes, and has been an evolutionary constant for all vertebrates (Doolittle and Surgenor, 1962; Doolittle, 1990). All vertebrate fibrinogens are large proteins with molecular weights between 320,000 and 400,000. They are composed of 3 pairs of polypeptide chains (α_2 β_2 γ_2) that vary in amino acid composition (Doolittle, 1990). The amino acids of the β and α chains are highly variable among species, but those of the γ chain are highly conservative among species (Doolittle, 1990). Since relatively high VCI values were associated with glochidia exposed to carp (non-host) plasma and fibrinogen (sheep) exposures, it is probable that the primary cue that stimulated these responses is found on the more conservative chain. The constituent components of fibrinogen could be tested in future chemosensory work using fragmentation procedures outlined by Spraggon *et al.* (1997).

Preliminary results with artificial media infer that plasma components may be important for increasing glochidial transformation success. Keller and Zam (1990) reported the transformation of glochidia to juveniles in an *in vitro* culture medium that included only serum. However, Hudson and Shelbourne (1990) reported that transformation rate for glochidia was increased with the inclusion of fish plasma. Isom and Hudson (1984) reported the importance of adding fish plasma to artificial media; glochidial transformation could occur in artificial media with plasma from confirmed non-host fish species. Their conclusion was that the key component in fish blood, necessary to initiate glochidial transformation, was contained in the blood of all fish tested. The important substance in plasma may be fibrinogen or related compounds. Fibrinogen may not be essential to transform glochidia, but substances in plasma that are not in serum seem to have a positive effect on transformation success, as well as a stimulatory effect on the behavior of glochidia. Our findings, that glochidia are strongly predisposed to respond to fibrinogen, suggest that further research on the hematological and immunological aspects of the parasite-host relationship between glochidia and fish is needed to isolate those blood components essential to both closure and transformation of glochidia on host fishes.

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Research Note

A new occurrence of *Anodontites soleniformis* Orbigny, 1835 in northeastern São Paulo State, Brazil (Bivalvia: Mycetopodidae)

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Abstract: A new occurrence of *Anodontites soleniformis* Orbigny 1835 is recorded for the first time in the Pardo River drainage. Thirty specimens were collected and the shell was compared with published figures. By the configurations and the layout of the shell we consider *A. soleniformis* as subgenus *Ruganodontites*. We note the presence of *A. soleniformis* in the Northeastern part of São Paulo State, Brazil.

Key Words: Bivalvia, Mycetopodidae, *Ruganodontites*

Thirty-one specimens of *Anodontites* sp. were collected while sampling local mollusks in the tributaries of the Pardo River, in the Ribeirão Preto region (NE State of São Paulo, Brazil).

The specimens have a superficial resemblance with those from Rio da la Paila (tributary of the Cauca river of the Rio Madaglena drainage, Colombia) recorded by Ortmann (1921) as *Anodontites crispata* Brugière, 1792. However, neither the literal description of *A. crispata* made by Ortmann (1921) ("shell not, or very little oblique, subtrapezoidal, rather elongated, with the lower margin straight or more or less concave (sinuated); epidermis dull, dark, not rayed, not smooth, but strongly and densely sculptured all over by concentric or radial, or irregular wrinkles; prismatic border narrow or wider, of nearly equal width") nor that of Marshall (1931a, Pl. 1, figs. 1-4: herein plate I) ("... radically different sculpture, arranged in distinctly radiating bands of beautifully regular, closely-set festoons, so disposed that they form also a concentric sculpture") fits with the morphology of the specimens in question, especially in the sculpture of the shell.

The surface sculpture was the very character adopted by Marshall (1931b) to differentiate subgenera in the *Anodontites*. Concerning this character, the Pardo River specimens (plate II, 1-2, plate III, 5) fit with the sculpture of the subgenus *Raganodontites*, which originally included the species *Anodontites (Ruganodontites) colombiensis* (cf. Marshall, 1930; 1931a, plate II, figs. 1, 3, 4 and 6: herein

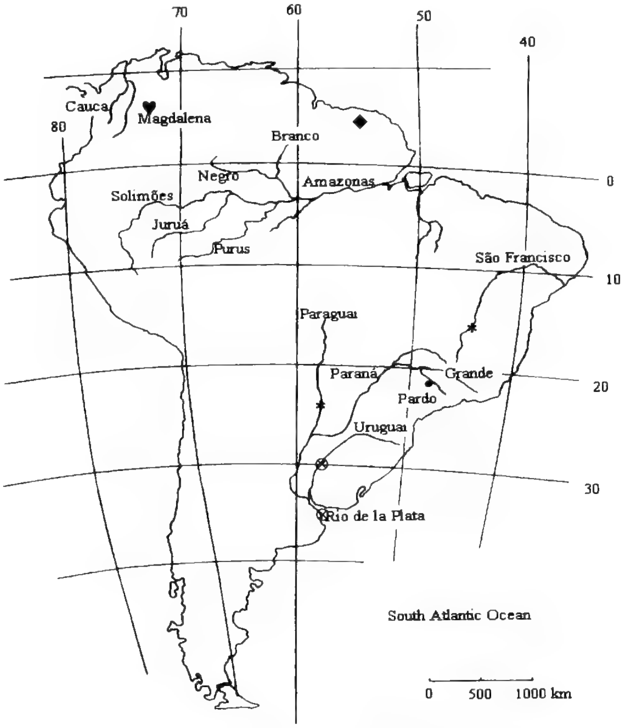

Fig. 1. South America map: (•) New distribuition of *Anodontites soleniformis* in South America; (∗) Distribution of *A. crispatus soleniformis* Orbigny Bonetto (1967); (♥)Type locality of *A. crispata* Brugière by Ortmann (1921); (◆)Type locality of *A. crispata* by Brugière, cited by Marshall (1931a); (⊗) Type locality of *A. crispatus tenebricosus* by Bonetto & Ezcurra (1965)

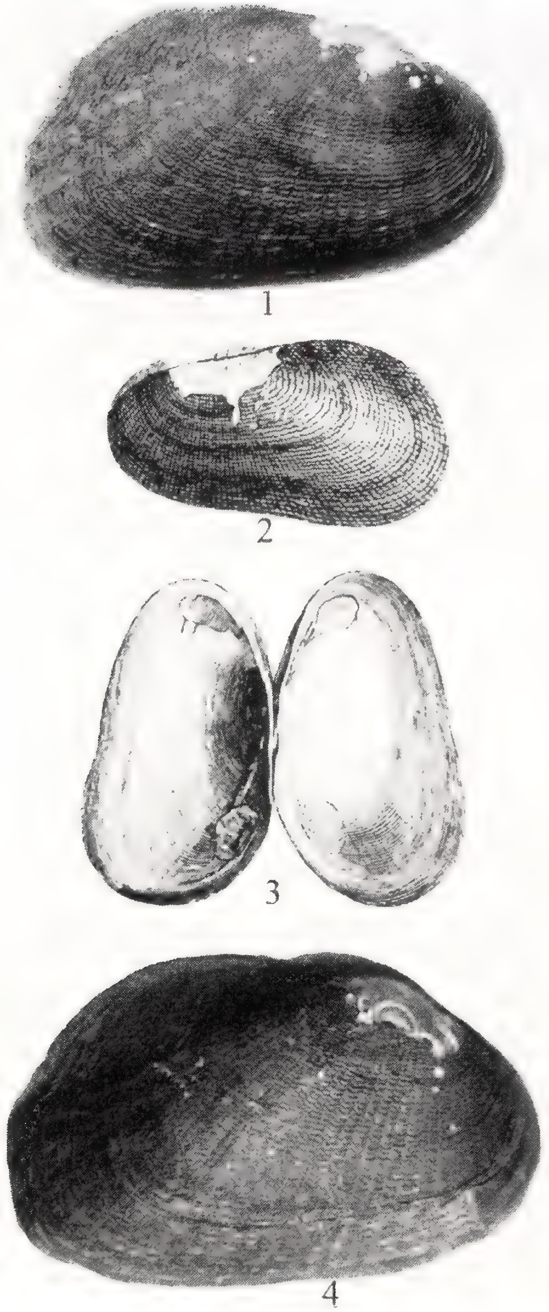

Plate I-1. *Anodontites crispata* Brugière, from Cayenne, French Guiana. U.S.N.M. N° 86402, x 1.9 diam. 2, 3. Photographic copies of Brugière's figures. 4 Lamarck's "type"of *Anodonta crispata* in the Paris Museum, x 1.4 diam.

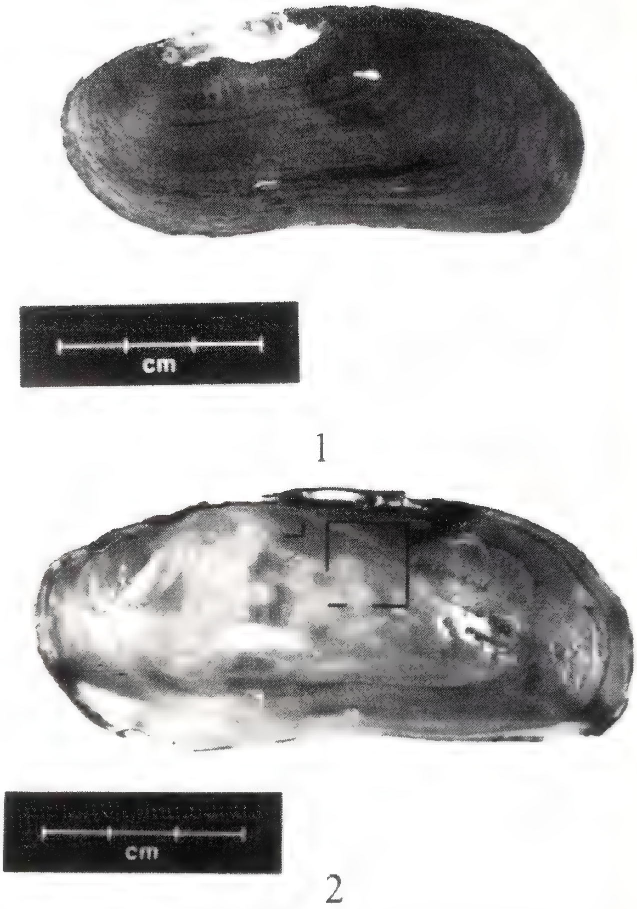

Plate II-1. *Anodontites soleniformis*, external view of the left valve showing the lines of growth and sculpture; 2. *Anodontites soleniformis*, internal view of the right valve, showing the muscle scar, ligament and ligamental sinus.

plate III), a species distributed on the western side of the Andes.

In a partial revision of the group, Bonetto & Ezcurra (1965), and Bonetto (1967) erected subspecies for the species *Anodontites crispatus*. Two of the these subspecies are distributed in Southern Brazil, nearby the Pardo River: *A. crispatus soleniformis* Orbigny, 1835 (Paraguay and Upper Paraná river) and *A. tenebricosus* (Lea) (lower Paraná River, Rio de la Plata, and Uruguay River) (Fig. 1). In this regard, the specimens of the Pardo River are related to those described as *A. crispatus soleniformis*. However, the specimens have the same sculpture described for *A. (Ruganodontites) colombiensis*, and consequently should be regarded as members of this group. Therefore, there is no need to adopt subspecific names in this case, and we prefer to consider the Pardo River specimens only as *A. soleniformis* or, considering the subgenus, as *A. (Ruganodontites) soleniformis*, being the first record of the taxon for the northeast of São Paulo State.

Anodontites soleniformis, Orbigny 1835.
New locality: Pardo River, Ribeirão Preto, São Paulo, Brazil 21°7'S, 47°45'W. Fig. 1
Habitat: muddy substrata

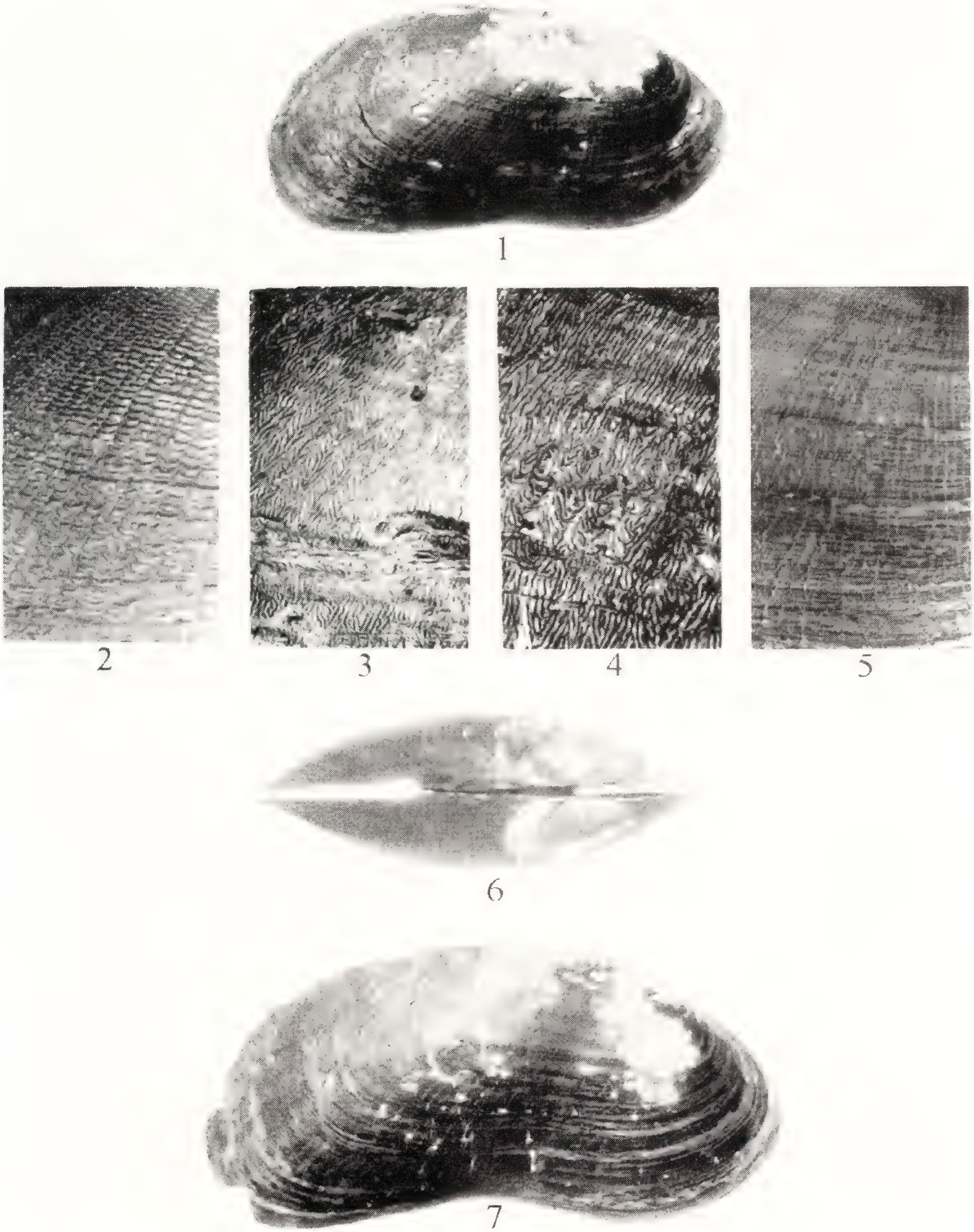

Plate III-1. *Anodontites colombiensis* Marshall; 2. *A. crispata* Brugière, from U.S.N.M. no. 86402; 3. *A. colombiensis* Marshall, sculpture of Ortmann's "A.crispata Brugière"; 4. *A. colombiensis* Marshall, sculpture of type; 5. *A. soleniformis* Orbigny, from author's collection; 6. *A. crispata* Brugière, dorsal view of U.S.N.M. no. 84402; 7. *A. colombiensis* Marshall. Type, 1.17 times natural size.

Collectors: Alvaro da Silva Costa and Wagner E. P. Avelar
Date: May 20, 1993, 29 specimens in the author's collection. Two specimens and one right valve are deposited as vouchers in Museum of Zoology USP number MZ 31329.

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Recent population changes in freshwater mussels (Bivalvia: Unionidae) and zebra mussels *(Dreissena polymorpha)* in Lake St. Clair, U. S. A.

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Abstract: To determine trends in abundances, we conducted a survey of freshwater mussels (Bivalvia: Unionidae) and zebra mussels (*Dreissena polymorpha* [Pallas,1771]) at five sites in the northwestern portion of Lake St. Clair in 1997. Previous, more extensive spatial surveys between 1986 and 1994 showed that unionids were mostly eliminated from the lake as a result of zebra mussel infestation, but at least a few unionids were still present in the northwestern portion in 1994. The 1994 survey also showed that zebra mussel densities were still increasing in this portion of the lake. In the present survey, no live unionids were collected despite a sampling effort modified from prior surveys specifically to locate live individuals. From these results, we believe that freshwater mussels have been eliminated from the open waters of Lake St. Clair. Zebra mussel populations appear to have reached a steady state in the northwest portion as evidenced by a decrease in mean density from 2,247 m^{-2} in 1994 to 1,237 m^{-2} in 1997, and a decrease in the mean size of individuals in the population. Although they were common in previous surveys, we did not collect any zebra mussels with a shell length > 20 mm.

Key Words: freshwater mussels, unionid extirpation, *Dreissena* infestation, mussel trends, Great Lakes

The introduction and rapid expansion of zebra mussels (*Dreissena polymorpha* [Pallas, 1771]) in North America has led to dramatic ecological changes in aquatic systems where this mussel has become abundant (for overviews on specific systems see Nalepa *et al.*, 1999; Strayer *et al.*, 1999). While most groups of aquatic organisms from bacteria to fish have been affected by the filtering activity and habitat alterations of large *D. polymorpha* populations, the taxonomic group most negatively impacted has been freshwater mussels of the family Unionidae (Bivalvia) (Schloesser *et al.*, 1996; Ricciardi *et al.*, 1998). Zebra mussels attach to the shells of unionids and subsequently impede normal metabolic activities (feeding, respiration, excretion) and burrowing behavior. In addition, large populations of zebra mussels can negatively affect unionids by filtering organic material from the water column thereby reducing amounts of available food (Strayer and Smith, 1996).

We have been documenting population trends of unionids in Lake St. Clair since 1986. In our first survey in that year, we found a diverse unionid community that had changed little since the turn of the century (Nalepa and Gauvin, 1988). Because the lake receives large inputs of high-quality water from Lake Huron and has a rapid flushing rate, habitat conditions tend to favor a diverse and stable fauna (Leach, 1991). Two years after our 1986 survey, the first zebra mussel reported in North America was discovered in the southeastern portion of the lake (Hebert *et al.*, 1989). We subsequently documented abundances of both unionids and *Dreissena polymorpha* in 1990, 1992, and 1994 (Nalepa, 1994; Nalepa *et al.*, 1996). Unionid populations first began to decline in the southeastern portion of the lake and then declined in the northwestern portion. This spatial trend closely paralleled the expansion of the *D. polymorpha* population from the southeast to the northwest over the same time period. In our first survey in 1986, we collected 281 unionids from 29 lakewide sampling sites. This number declined to 248 in 1990, to 99 in 1992, and to six in 1994 (Nalepa *et al.*, 1996). Further, while unionids were found at 25 of 29 sites in 1986, they were collected from only four sites in 1994. All four sites were located in the northwestern region of the lake. Mean densities of *D. polymorpha* in the northwestern portion increased dramatically between 1990 and 1994 (Nalepa *et al.*, 1996).

We present the results of an abbreviated survey of unionid and *Dreissena polymorpha* populations conducted in the northwestern portion of the lake in 1997. The objectives of the survey were to determine whether any unionids

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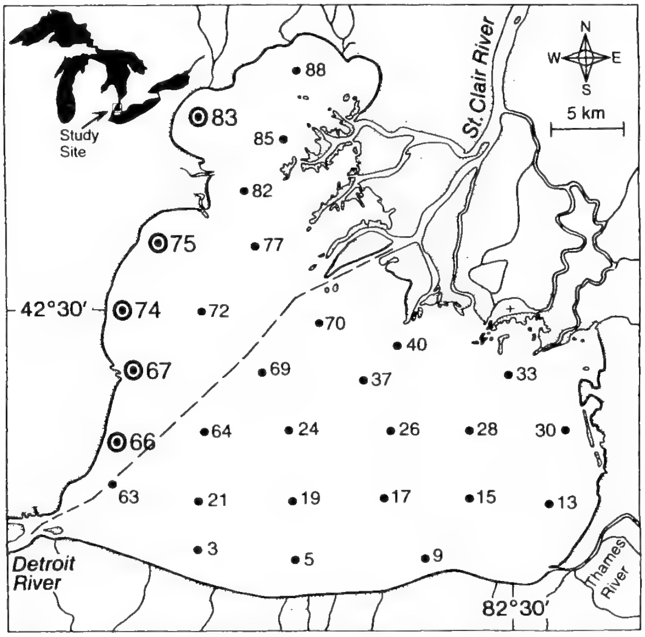

Fig. 1. Location of sampling sites in Lake St. Clair. The circled sites were the sites sampled in 1997 (this study), and all sites were sampled in 1986, 1990, 1992, and 1994. Dashed line represents the shipping channel.

remained in this portion of the lake, and to document density trends in *D. polymorpha* between 1994 and 1997.

METHODS

The sites sampled in 1997 were Stations 66, 67, 74, 75, and 83 (Fig. 1). These sites were located near the western shoreline and were among the last sites to be heavily colonized by zebra mussels. Site designations and locations are the same as those given in Pugsley *et al.* (1985). Details of the sampling protocol are given in Nalepa (1994). Briefly, at each site divers positioned a 0.5 m^2 frame on the bottom and hand-collected all hard material within the frame area to a depth of about 5 cm. Ten replicate samples were taken at each site with divers moving about 2-3 m into the current between replicates. All material collected in a replicate was put into a fine mesh bag, supported within a crate, and then brought to the surface. Substrate material was immediately examined for live unionids. *Dreissena polymorpha* were removed from the substrate (dead unionid shells, rocks, plant material), washed through a 500-um mesh screen, and preserved in 5% formalin.

Using information from our survey in 1994, we knew unionids would be rare in 1997. Therefore, we also surveyed the unionid population using the "diver-transect" method (Isom and Gooch, 1986). At each site, a weighted line 100 m in length was stretched along the bottom, and divers swam on each side of the line searching for unionids. As the divers swam, they slid a measuring rod along the line that extended out from the line 1 m on each side. The area searched for unionids by this method was 200 m^2 per site.

For each of the 10 replicate quadrat samples taken in 1997, up to 500 *Dreissena polymorpha* were counted. Replicates with a greater number of mussels were proportionally split, counted, and the portion applied to the entire sample. Shell lengths of mussels in five of the replicate samples were measured by first placing each cleaned individual onto a clear plastic sheet, and then placing the sheet onto a scanner. The scanning program provided total shell length of each individual. For length-frequency distributions, mussels with a shell length > 5 mm were placed into size categories of 1-mm intervals, while mussels with a shell length < 5 mm were placed into a single size category. In the previous surveys, individuals in all 10 replicates were measured using a digitizer pad.

RESULTS AND DISCUSSION

No live unionids were collected at any of the five sites sampled in 1997 (Fig. 2). While this finding further reinforces our earlier conclusion that unionids have essentially been extirpated from the open waters of the lake (Nalepa *et al.*, 1996), the results are noteworthy because our sampling design was specifically modified to find live animals. In our four earlier surveys, our main objectives were to assess trends in densities, species composition, biomass, and distribution patterns of unionids. The quadrat

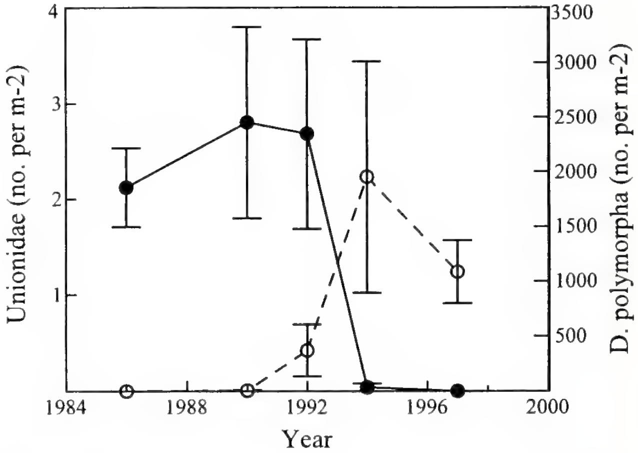

Fig. 2. Mean (± SE) density (no. m^{-2}) of Unionidae and *Dreissena polymorpha* at the five sites sampled in 1997. Densities in 1986, 1990, 1992, 1994 were taken from Nalepa *et al.* (1996). Note that the two taxa have different scales. Unionidae = solid circle, *D. polymorpha* = open circle.

sampling method was employed because it provided the most suitable method to meet these objectives given limited resources (Kovalak *et al.*, 1986). The 29 sites sampled in earlier surveys were systematically located throughout the lake (Fig. 1), and the 10 replicates per site were the minimum needed to provide reliable estimates of population densities (Downing and Downing, 1992). Given the number of sites and replicates, the total area sampled in each of these earlier surveys was only 145 m^2 (10 replicates per site x 0.5 m^2 per replicate x 29 sites). In contrast, the main objective of the 1997 survey was to assess the presence/absence of unionids. Thus, we sampled a much broader area (1,000 m^2 with diver-transect method and 25 m^2 with quadrat method), and limited our efforts to the northwestern portion of the lake where at least some live unionids were found in 1994. We also sampled at sites located nearest to shore where, according to our earlier surveys, densities tended to be greater (Nalepa *et al.*, 1996). Thus, despite a sampling effort purposely designed to find live mussels, none were found. With these findings, it can be stated with some certainty that unionids have been extirpated from the open waters of Lake St. Clair.

Regression models have shown a direct relationship between densities of *Dreissena polymorpha*, the number of *D. polymorpha* attached to unionids, and unionid mortality (Ricciardi *et al.*, 1995). Unionid mortality increases significantly when *D. polymorpha* densities are greater than 1,000 m^{-2}, and extirpation occurs in a few years when mean densities are over 6,000 m^{-2} or 100 per unionid. Further work by Ricciardi *et al.* (1996) showed that mortality can occur with infestations as low as 10 per unionid if attached *Dreissena* are large relative to the unionid. As noted by Nalepa *et al.* (1996), the decline in unionids relative to increased numbers of *D. polymorpha* in Lake St. Clair appeared to fit model predictions very well, but mortality also occurred at some sites where the number of *D. polymorpha* was very low. For instance, unionid densities at Station 83 were 2-4 m^{-2} in 1986, 1990 and 1992. In 1994, unionid density declined to 0 m^{-2} even though the mean density of *D. polymorpha* at this site was only 150 m^{-2}, and the mean number of *D. polymorpha* found attached to unionids was only six. Clearly, *D. polymorpha* can adversely affect unionids in ways other than by direct attachment to the shell. In the Hudson River, unionid populations declined by 59% after *D. polymorpha* became established, although there were few individuals found attached to unionid shells (Strayer and Smith, 1996). It was concluded that the main reason for the unionid decline was a decrease in food availability. In Lake St. Clair, chlorophyll levels declined 2-fold after *D. polymorpha* became abundant (Nalepa *et al.*, 1993), and could have also contributed to the unionid decline.

As found in Lake St. Clair, studies of *Dreissena*-induced mortality in other systems have shown that unionid populations are usually reduced > 90 % within 4-8 years after *D. polymorpha* first becomes established (Ricciardi *et al.*, 1998). The evidence suggests that if zebra mussels are present and able to persist on exposed unionid shells, extirpation of unionids will likely occur over time. On the other hand, other studies have shown that unionids could still be found in certain habitats where *D. polymorpha* attachment is not consistent. For example, some unionids were found in shallow waters (1-2 m) of western Lake Erie despite the presence of *D. polymorpha* and the extirpation of unionids in deeper waters (Schloesser *et al.*, 1997). In these shallow habitats, it was postulated that wave action, water level fluctuations, and winter ice scour either prevented mussels from permanent attachment, or induced zebra mussels to release after initial colonization. In another study, Nichols and Wilcox (1997) found unionids devoid of attached zebra mussels in the soft sediments of a wetland area in western Lake Erie. They noted that unionids in the wetland burrowed into the soft sediments during at least part of the day to avoid high summer temperatures (up to 27°C). It was hypothesized that this burrowing behavior prevented *D. polymorpha* from attaching, or killed any individuals already attached. At this point, it is not clear whether these areas represent permanent unionid refugia, or are merely habitats where extirpation has been delayed. The study in nearshore western Lake Erie was conducted in 1993

Table 1. Mean (±SE) density (no. m^{-2}) of *Dreissena polymorpha* at the five sites in Lake St. Clair that were sampled in 1997. Densities in 1990, 1992, and 1994 were taken from Nalepa *et al.* (1996). Differences between two successive years at each site were tested with the t-test (log +1 transformed). An asterisk indicates density is significantly different (P < 0.05) from the density of the previous year.

	Station					
Year	St. 66	St. 67	St. 74	St. 75	St. 83	Mean
1990	0	0	0	0	2	< 1
1992	136 ± 35*	116 ± 20*	389 ± 143*	1466 ± 253*	27 ± 10*	427
1994	6502 ± 504*	3295 ± 1148*	296 ± 58	991 ± 172	150 ± 81	2247
1997	1268 ± 139*	867 ± 163	1874 ± 295*	1992 ± 1086	182 ± 48	1237

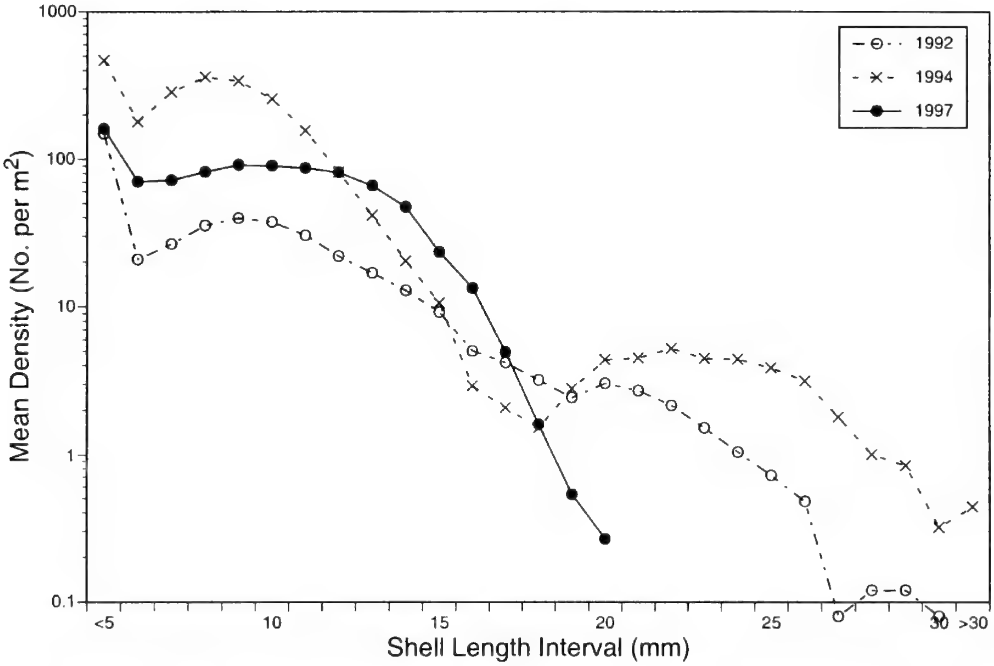

Fig. 3. Size-frequency distribution of *Dreissena polymorpha* in 1992, 1994, and 1997 at each of the five sites sampled in 1997. The scale for the ordinate is logarithmic. 1992 = open, 1994 = hatched, 1997 = solid circle.

(Schloesser *et al.*, 1997), or just five years after *D. polymorpha* became abundant. We still found unionids in Lake St. Clair in 1994, or six years after *D. polymorpha* became abundant, but did not find any unionids three years thereafter. Obviously, follow-up surveys in areas where unionids have been found in the presence of *D. polymorpha* are essential.

Overall, mean densities of *Dreissena polymorpha* at our five sampling sites declined between 1994 and 1997, but there was great variation at individual sites (Table 1, Fig. 2). Densities at the two southernmost sites (Stations 66 and 67) increased between 1992 and 1994 to reach maximum densities, but then declined in 1997. Densities at the three sites located farther north (Stations 74, 75, and 83) were relatively low in 1994, but then increased in 1997. These temporal patterns in abundance are consistent with earlier surveys that showed populations of *D. polymorpha* in Lake St. Clair expanded from southeast to northwest as related to water flow regimes (Nalepa *et al.*, 1996). A high volume of water enters the lake from the St. Clair River, flows through the lake mostly along the shipping channel, and then exits via the Detroit River. This flow pattern impedes zebra mussel larvae in the southeast from easily colonizing the northwest. Based on density trends at individual sites between 1992 and 1997, it would appear that expansion has diminished in the northwestern portion of the lake, and populations are likely approaching an equilibrium with the surrounding environment. Populations reached a similar steady state in the southeastern portion by 1994 (Nalepa *et al.*, 1996). Thus, zebra mussel populations in both the southeastern and northwestern portions of the lake appear to have reached equilibrium within 5-6 years of initial colonization.

A further indication that populations have stabilized in the northwestern portion of the lake is denoted by a decrease in the mean size of individuals in the population (Fig. 3). Generally during the initial years of population expansion, year classes (cohorts) are clearly defined (Griffiths *et al.*, 1991; Nalepa *et al.*, 1995). However, as food resources decline, growth rates slow and older-year classes become indistinct from the younger cohorts. Since metabolic costs increase with size, lower food availability affects large individuals more than small (Walz, 1978 a, b). As a result, overall mean size of individuals within the population declines. Although temporal trends in abundances varied between sites, a clear trend to smaller individuals was apparent (Fig. 3). Yearly size-frequency distributions were significantly different for each of the sites and for all sites combined (G-test; $P < 0.05$). In 1992 and 1994, size-frequency distributions were bimodal (Fig. 3). There was a peak of individuals at 8-11 mm in shell length and another peak at 19-25 mm, which implies a two year life span. By 1997, the modal peak of larger individuals was no longer evident and, in fact, no individuals larger than 20 mm were collected at any of the sites.

In summary, no live unionids were collected in the open waters of Lake St. Clair despite sampling efforts specifically designed to locate living individuals. Unionids began to decline within two years of when *Dreissena polymorpha* was first recorded in the lake in 1988, and this latest survey tends to confirm that the loss in the open waters is now complete. Future surveys must now focus on surrounding wetland areas that may serve as refugia for surviving populations as found in western Lake Erie. It has been suggested that unionids in such refugia may serve as brood stock to recolonize lake areas if zebra mussel populations ultimately decline (Nichols and Wilcox, 1997). While populations of *D. polymorpha* have now apparently reached a steady-state in Lake St. Clair, future surveys will determine whether populations will decline from present levels and, if so, whether the decline would be sufficient to allow unionids to recolonize.

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An Evaluation of Air and Water Transport of Freshwater Mussels (Bivalvia: Unionidae)

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Abstract: To compare the stress of transportation of mussels in water versus in air, we collected in the field fifty specimens of each of five species: *Elliptio complanata, Villosa iris, Fusconaia ebena, Quadrula quadrula,* and *Amblema plicata.* We froze subsamples of each species in liquid nitrogen and the rest of the animals were divided into two groups. One group was placed in a water-filled, aerated tank and the other group was placed in coolers with wet burlap before all were transported to the laboratory. We removed a subsample of each group at 6 hr intervals up to 24 hr, and froze it in liquid nitrogen. We used changes in the concentration of glucose and glycogen in the posterior adductor muscle, gill, and mantle to estimate the stress caused by the transport and holding methods.

Villosa iris was the most sensitive to the effects of transportation, particularly as reflected by glucose concentrations in the mantle and posterior adductor muscle. Glucose became elevated in both air-transported specimens of this species, but the change was significantly greater in those transported in air. *V. iris* is found in well aerated habitats, and previous studies have documented its greater sensitivity to reduced oxygen than most other species. The other unionids we tested tended to show significant elevations in glucose only in air-transported specimens, with the extent of increase varying with the species. Glycogen concentrations did not change significantly in any of the species during transportation in either mode. Overall, transportation in water appeared to be less stressful than in air, but for short intervals of time, it may not matter for species such as *Fusconia ebena*, which are relatively tolerant of oxygen lack.

Key Words: Unionids, transportation, stress, glycogen, glucose, mollusks, bivalves

The freshwater mussel fauna (Superfamily Unionacea) in the United States has experienced a precipitous decline in abundance during this century, the decline stemming principally from anthropogenic alterations of physical habitat and water quality. Because of continuing declines in mussel populations and the recognition of 69 federally endangered and threatened mussel species, protected under the Endangered Species Act of 1973, state and federal resource agencies have become actively involved in conservation efforts. Relocation of mussels has become a widely accepted technique to recolonize stream reaches decimated by previous pollution events (Ahlstedt, 1979; Sheehan *et al.*, 1989), to salvage specimens from construction projects (Oblad, 1980; Dunn, 1993), to restore populations of endangered species (O'Beirn *et al.*, 1998), and to prevent loss of populations through colonization by zebra mussels [*Dreissena polymorpha* (Pallas, 1771)]. In a recent review of relocation projects, Cope and Waller (1995) noted high mortality in most relocation efforts and little guidance on standard methods for relocation or for monitoring relocation success. While high mortality following transportation could be due to poor conditions in the receiving waters (*e. g.*, low dissolved oxygen), the physiological impact of the transportation process itself has seemingly not been investigated.

Although mussel relocations have been conducted routinely for nearly 30 years, there has been no adequate assessment of the modes of transport from one location to another. Waller *et al.* (1995) conducted a relocation of mussels in the upper Mississippi River and noted a decreasing trend in survival with duration of aerial exposure in June compared with September. These authors concluded that handling and aerial exposure should have no major effect on survival of mussels in moderate air temperatures, if mussels are collected and processed within several hours. However, no physiological indicators of condition or stress in their mussels were monitored, only survival. The subsequent survival of mussels following translocation is affected by the stress of the transport itself as well as the charac-

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teristics, such as dissolved oxygen, temperature, pollution, etc. of the habitat to which they were moved.

Our study was conducted to compare the degrees of stress caused by transporting mussels in air versus in water, and to determine to what extent different species vary in their responses. Biochemical analyses of free glucose and glycogen in body tissues were used to assess the level of stress in five species from diverse habitats by the two transport methods.

METHODOLOGY

We collected unionids either by SCUBA diving in lakes, or by snorkeling in streams. Three freshwater mussel species, ebonyshell (*Fusconaia ebena* I. Lea, 1831), mapleleaf (*Quadrula quadrula* Rafinesque, 1820), and threeridge (*Amblema plicata* Say, 1817) were obtained from Kentucky Lake, Tennessee in cooperation with the Tennessee Shell Company and the Tennessee Wildlife Resources Agency in July 1996. We collected specimens of the rainbow mussel (*Villosa iris* I. Lea, 1829) from Copper Creek, Virginia and the eastern elliptio (*Elliptio complanata* Lightfoot, 1786) from the Nottoway River, Virginia in September 1996.

Fifty specimens of each species were collected, and a subsample (5-6) of these was frozen in the field by opening the shell and immersing specimens in liquid nitrogen (-195°C) for a few seconds until thoroughly frozen. For technical reasons, it was not practical to freeze the mussels immediately after bringing them up from the lake or river bottom. The subsequent delay of 15 to 60 minutes (depending on species) means that the zero-time glucose concentrations may be higher than in situ, although the animals were kept in buckets of water during this delay. All frozen mussels were then transferred to coolers with dry ice (-56°C) and subsequently placed in a freezer (-80°C) upon arrival at the laboratory. Half of the remaining animals were placed in a water-filled, aerated transport tank (transportation in water), and the other half were placed in coolers with wet burlap (transportation in air) and transported to the laboratory.

For the unionids transported in water and air, at intervals of 6, 12, 18, and 24 hr, a subsample of each species was removed and quickly frozen in liquid nitrogen, then stored at -80°C until analyzed. On the basis of pilot studies (Chen *et al.*, 1996), we chose three tissues (posterior adductor muscle, gill and mantle) and two metabolites (glucose and glycogen) for estimating the stress response of the mussels. Increases in glucose probably reflect short-term stress (Pekkarinen and Suoranta, 1995), and glycogen represents the primary energy store and is one measure of the relative health of mussels (deZwaan, 1983).

In preparation for biochemical analysis, the three tissues were dissected out, weighed, homogenized in 6% perchloric acid, neutralized with potassium bicarbonate, and the extract was stored at -80°C. Free glucose was measured first on the extract, and then glycogen was determined by the enzymatic method of Keppler and Decker (1984). Sigma kits (Catalog No. 510-A, Sigma Chemical Co., St. Louis, Missouri) were used for measuring the free glucose and that released after enzymatic breakdown of the glycogen.

Statistical analyses were conducted by unpaired Student's t-test, comparing pre-transport and post-transport results, and the results of transportation in water versus transportation in air. The criterion for statistical significance was $p < 0.05$.

RESULTS

Glucose

Villosa iris. Both transportation in water and in air caused an initial elevation in glucose concentrations in the mantle tissue (Fig. 1). However, for those mussels transported and held in water, the mantle glucose concentrations recovered after they reached a peak at 12 hr, whereas those transported in air did not recover. Similarly, mussels transported in air had glucose concentrations in the posterior adductor muscle that were significantly higher than initial levels. Glucose concentrations were significantly higher in air-held versus water-held mussels at 18 hr and 24 hr.

Elliptio complanata. Transportation in water caused no significant elevation in glucose concentrations (Fig. 2), but there were obvious increases in glucose in mussels transported in air. The glucose concentrations of animals transported in air were significantly higher than those transported in water for the mantle tissue at all sample periods, and for the posterior adductor muscle at 18 hr.

Fusconaia ebena. Glucose concentrations of the three different tissues in this species did not change during the transportation in water, but increased significantly in specimens transported in air (Fig. 3). The changes in the posterior adductor muscle were the most noteworthy at 12 hr and 18 hr.

Quadrula quadrula. The glucose concentrations of specimens transported in air were significantly higher than those transported in water for some of the tissues at particular time periods; however, results were too inconsistent to provide an obvious trend (Fig. 4). Glucose levels in mantle tissue actually decreased during the 24 hr holding period.

Amblema plicata. The glucose concentrations of those transported in water increased significantly in the gill tissue after 18 hr, but there was a trend of decreasing glucose in the mantle and posterior adductor muscle (Fig. 5). In those specimens transported in air, glucose increased and then recovered to initial levels in gill and mantle tissue.

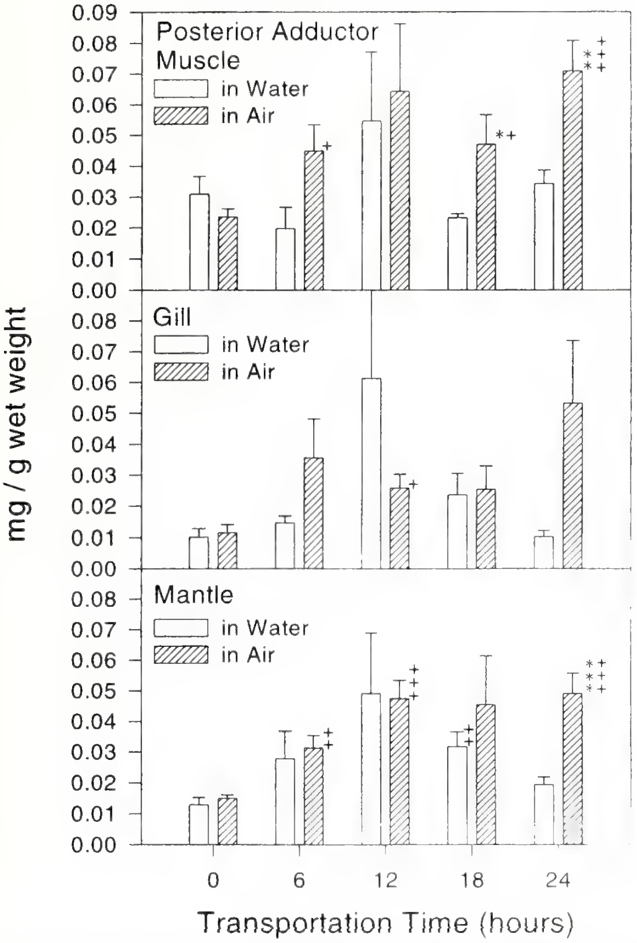

Fig. 1. Changes in glucose concentration in *Villosa iris* for three tissues under two different modes of transport. Error bars = ± SEM. N= 5. For the unpaired t-test, * $P < 0.05$, **$P < 0.01$, and ***$P < 0.005$ were used for the comparison between the glucose levels of mussels transported in air and water; + $P < 0.05$, ++ $P < 0.01$, and +++ $P < 0.005$ were used for the comparison between time 0 and the other transportation times.

Glycogen

Glycogen concentrations were variable, with no significantly consistent trends evident during the 24 hr of either transportation mode (Table 1). It is noteworthy that the mantle tissues have considerably higher concentrations of glycogen than the other tissues in all of the species tested.

DISCUSSION

Our results indicate that transportation in air generally was more stressful than transportation in water for all of the five species tested. The severity of the stress response by the animals, as reflected in the extent of glucose elevation, was seemingly related to the availability, or lack thereof, of dissolved oxygen in the typical habitat of a given species. *Villosa iris*, which is usually found in riffle areas of rivers having high dissolved oxygen concentrations, was the most sensitive to the transportation stress. Even transportation in water resulted in elevated glucose levels in mantle tissue of this species for the first 12 hr. On the other hand, species that live in areas experiencing relatively low dissolved oxygen conditions seemed to be more tolerant of transportation. Transportation in water did not result in obvious changes in glucose for *Elliptio complanata* (found typically in slowly flowing rivers) and the other three species sampled from Kentucky Lake, Tennessee. The mapleleaf (*Quadrula quadrula*) is found in medium to large rivers and reservoirs with a mud, sand, or gravel bottom; the ebonyshell (*Fusconaia ebena*) is found in sand and gravel of large rivers and reservoirs; and the threeridge (*Amblema plicata*) is found in small to large rivers and impoundments in mud, sand, or gravel.

Elevated glucose concentrations in hemolymph or tissues during environmental hypoxia or handling stress (as

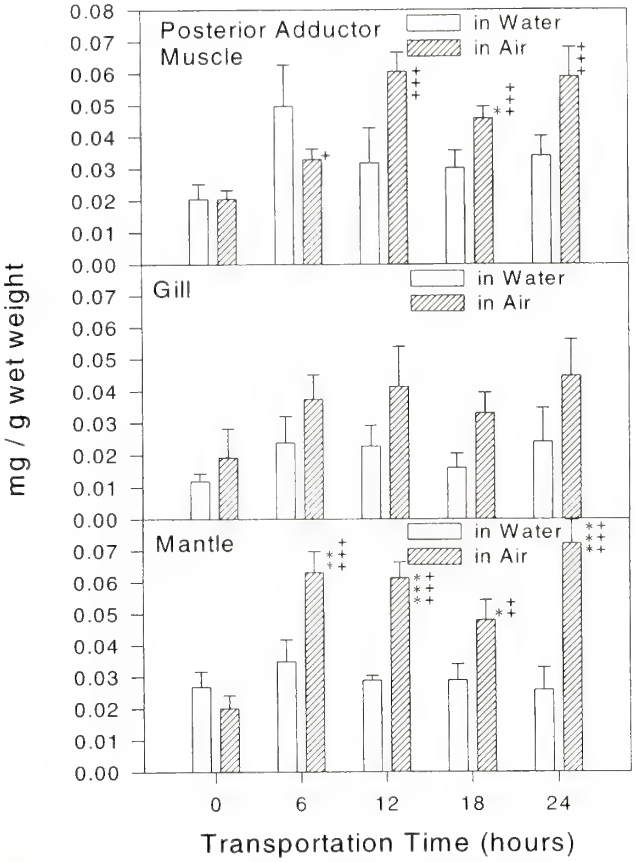

Fig. 2. Changes in glucose concentration in *Elliptio complanata* for three tissues under two different modes of transport. Error bars = ± SEM. N = 5. Statistical comparisons as in figure 1.

Table 1. Mean glycogen concentrations in unionids before and during transportation in water and in air. Values are in mg/g wet weight with SEM in parentheses. N = 5; PAM = posterior adductor muscle.

Method	Tissue	Sample Period				
		0 hr	6 hr	12 hr	18 hr	24 hr
				Villosa iris		
Water	Gill	1.73(0.35)	1.20(0.28)	0.98(0.26)	1.11(0.23)	1.14(0.21)
Air	Gill	1.18(0.29)	1.12(0.29)	0.95(0.17)	1.30(0.39)	2.40(0.67)
Water	Mantle	5.65(2.34)	11.08(2.69)	5.23(1.61)	10.17(2.15)	5.44(2.22)
Air	Mantle	5.84(1.52)	8.48(3.22)	5.59(1.14)	10.66(3.00)	3.37(0.89)
Water	PAM	3.45(0.70)	3.59(0.83)	3.46(0.73)	4.86(0.31)	2.08(0.52)
Air	PAM	2.28(0.51)	3.55(0.45)	3.00(0.68)	4.92(1.46)	3.33(0.32)
				Elliptio complanata		
Water	Gill	1.52(0.17)	1.24(0.22)	2.21(0.29)	2.30(0.28)	2.13(0.28)
Air	Gill	2.07(0.45)	1.08(0.10)	2.03(0.46)	2.66(0.10)	2.78(0.17)
Water	Mantle	11.77(1.38)	27.80(7.26)	19.78(2.80)	25.74(0.77)	20.03(2.75)
Air	Mantle	18.66(5.06)	23.76(4.78)	20.81(2.90)	24.06(6.28)	39.557(10.37)
Water	PAM	5.97(0.83)	7.51(0.54)	6.41(0.50)	7.36(0.59)	6.80(0.60)
Air	PAM	5.88(0.37)	6.84(0.91)	7.59(0.88)	9.18(1.13)	7.64(0.67)
				Fusconaia ebena		
Water	Gill	4.97(1.25)	4.16(0.91)	3.03(0.25)	4.99(1.86)	8.42(2.53)
Air	Gill	4.34(0.79)	3.53(0.71)	4.36(1.00)	2.55(0.43)	5.35(2.75)
Water	Mantle	137.88(12.62)	120.68(7.75)	113.35(7.32)	122.86(14.94)	125.02(8.31)
Air	Mantle	127.16(4.09)	119.19(7.66)	131.27(11.1)	134.22(14.04)	116.48(7.02)
Water	PAM	13.13(0.92)	11.93(1.87)	10.9(1.53)	12.42(0.68)	13.15(2.26)
Air	PAM	9.93(0.41)	14.79(1.61)	13.93(2.91)	15.78(2.89)	16.84(1.41)
				Quadrula quadrula		
Water	Gill	3.53(0.26)	4.03(1.23)	6.72(2.98)	4.23(0.85)	4.87(1.59)
Air	Gill	3.51(0.29)	6.11(2.44)	5.30(0.43)	2.48(0.55)	2.80(0.52)
Water	Mantle	75.71(3.48)	64.85(17.8)	61.20(12.95)	66.27(17.06)	49.38(12.58)
Air	Mantle	68.61(5.39)	65.44(8.11)	76.46(14.13)	63.66(16.31)	14.50(11.91)
Water	PAM	12.62(2.59)	9.17(1.95)	14.23(2.82)	7.09(1.67)	12.14(2.76)
Air	PAM	11.80(1.73)	15.09(3.29)	14.12(3.03)	13.24(2.49)	11.56(3.54)
				Amblema plicata		
Water	Gill	22.8(0.34)	3.26(0.81)	4.36(1.50	3.86(0.37)	4.28(1.33)
Air	Gill	2.12(0.68)	2.42(0.19)	2.84(0.58)	2.95(0.31)	3.52(0.57)
Water	Mantle	38.68(7.33)	44.03(7.86)	34.49(7.48)	36.17(6.45)	38.50(5.80)
Air	Mantle	26.22(8.03)	35.85(5.35)	43.99(9.40)	31.61(5.50)	52.33(12.82)
Water	PAM	7.52(0.53)	9.28(1.52)	8.54(1.36)	11.85(1.09)	7.28(1.24)
Air	PAM	7.54(2.12)	10.61(1.96)	11.39(2.34)	9.39(1.27)	13.64(3.44)

was seen in this study) have been observed in various invertebrates such as arcid clams (de Vooys *et al.*, 1991; de Zwaan *et al.*, 1995), terrestrial snails (Marques and Falkmer, 1976), freshwater snails (Wijsman *et al.*, 1988) and arthropods (*e. g.*, Kleinholtz and Keller, 1979; Mordue and Stone, 1979). The effects of transportation stress in water (duration not specified) were studied in *Anodonta anatina* by Pekkarinen and Suoranta (1995), who found that the glucose concentrations in the hemolymph and extrapallial fluids rose about 5-fold when mussels were transferred to the laboratory from the collecting site. The elevations of glucose in hemolymph and tissues are probably induced by hyperglycemic neurohormones that have been found in molluscs such as the marine bivalve *Mytilus edulis* (Robbins *et al.*, 1990) and freshwater snail *Lymnaea stagnalis* (Wijsman *et al.*, 1988; Hemminga *et al.*, 1985). These hormones act in a manner similar to the stress hormones (epinephrine and cortisol) of vertebrates, causing a mobilization of glycogen into glucose (Sumpter, 1997).

Changes in the concentrations of glycogen in the tissues of molluscs have been widely used as an assessment of their energy status and general physiological condition (Holopainen, 1987; Hemelraad *et al.*, 1990; Patterson *et al.*, 1997; Naimo *et al.*, 1998). Furthermore, the ability to tolerate acute hypoxia, and the anaerobic metabolic capacity of an animal, are seemingly related at least in part to the

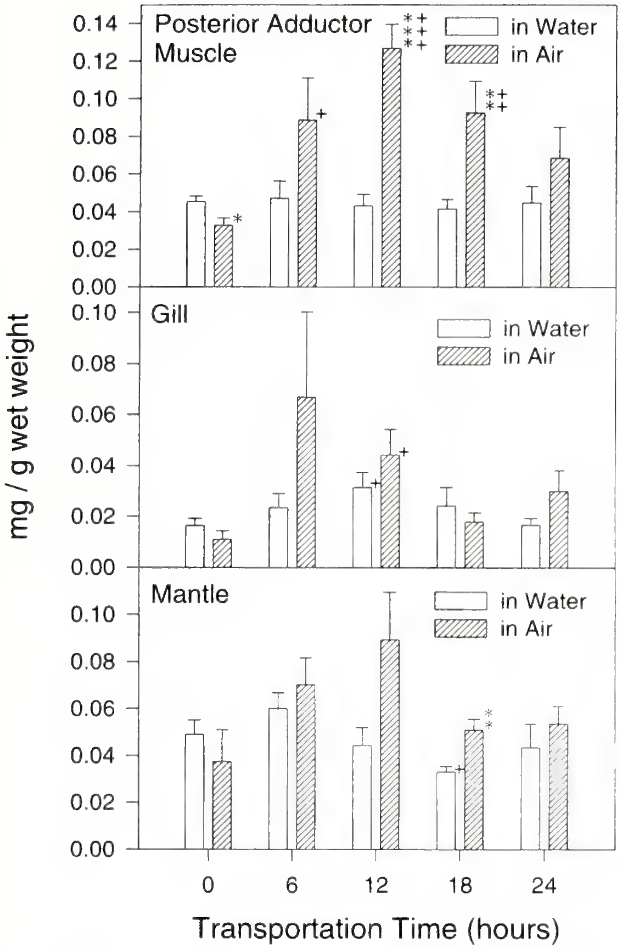

Fig. 3. Changes in glucose concentration in *Fusconaia ebena* for three tissues under two different modes of transport. Error bars = ± SEM. N = 5. Statistical comparisons as in figure 1.

glycogen concentrations in tissues. Hochachka (1982) compared the glycogen content of a variety of animals including *Mytilus edulis*, turtles, and some fish species and concluded that animals with high anaerobic capacity normally have high glycogen levels in different tissues. In other studies done in our laboratory, we also found that species [such as *Elliptio complanata* and *Pyganodon grandis* (Say, 1829)] which are more tolerant of low dissolved oxygen, usually have higher concentrations of glycogen in the tissue. The glycogen content of the mussels in our study did not decline during the 24 hr in either transportation mode. This result is likely because the glycogen consumed through anaerobic metabolism was small in comparison to the high storage concentrations of glycogen. It is also reassuring that glycogen did not decline during transport of the duration we tested.

The ebonyshell specimens exhibited increasing glucose levels in the posterior adductor muscle, which reached a maxium at 12 hr but declined thereafter. The results imply that *Fusconaia ebena* uses considerable energy in closing the valves during the first few hours of transport. The other two species collected from Kentucky Lake also seemed to tolerate transportation in air and exhibited a rise and subsequent decrease in glucose, somewhat similar to that of *F. ebena*. There are two possible explanations for the decline in glucose in the later period; one is the shift to alternative anaerobic metabolic pathways that use amino acids. For example, aspartate is used in the anaerobic metabolism of many marine bivalves (Kreutzer *et al.*, 1985; Demers and Guderley, 1994). However, it was found that the Asian clam *Corbicula fluminea* (Müller, 1774) does not catabolize amino acids during emersion (Byrne, 1988); hence, freshwater mussels might not use aspartate for anaerobiosis. The other possible explanation for the decline of glucose over time is the reduction of overall metabolism. We determined previously that the giant floater (*Pyganodon*

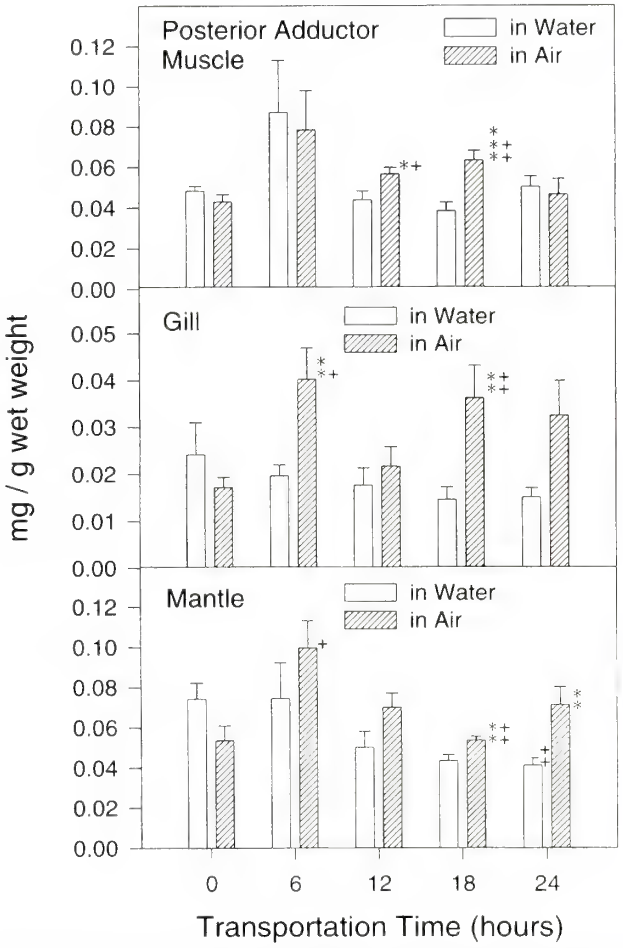

Fig. 4. Changes in glucose concentration in *Quadrula quadrula* for three tissues under two different modes of transport. Error bars = ± SEM. N = 5. Statistical comparisons as in figure 1.

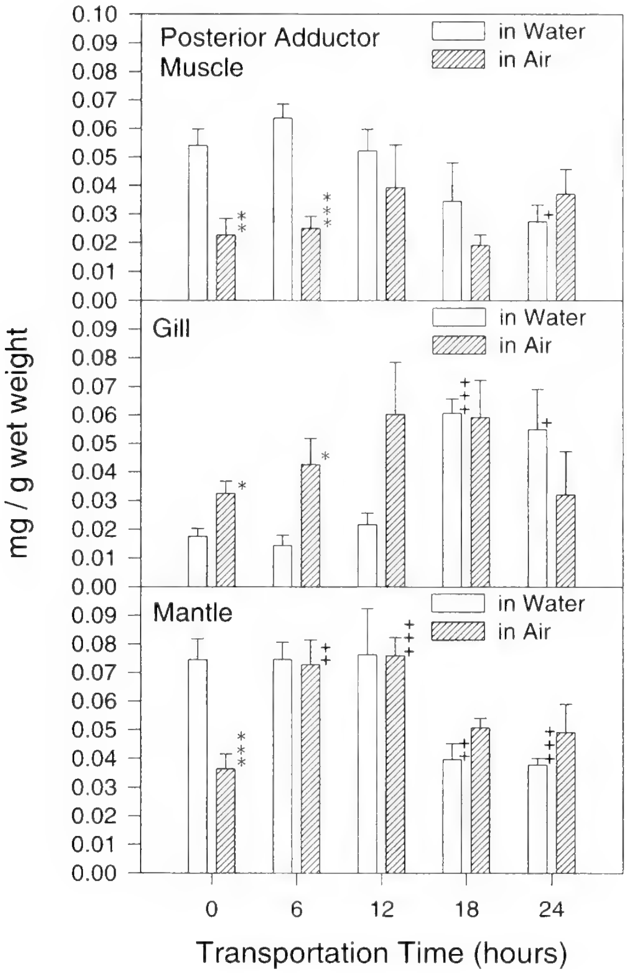

Fig. 5. Changes in glucose concentration in *Amblema plicata* for three tissues under two different modes of transport. Error bars = ± SEM. N = 5. Statistical comparisons as in figure 1.

grandis), an hypoxia-tolerant mussel found in the benthic area of lakes, can drastically reduce its heart rate when dissolved oxygen becomes very low (Heath and Chen, 1996). Some marine bivalves can reduce energy metabolism to increase resistance to emersion in air (Storey, 1988; Wang and Widdows, 1993).

As mussels are strictly aquatic, it can be assumed that transportation in water would be less stressful, especially since the water for transport was aerated. However, transportation in water requires more space, and aeration facilities may be required. In contrast, transportation in air with wet burlap does not require as much equipment and is not especially stressful for the oxygen-tolerant species for up to at least 24 hr. It has been reported that *Fusconaia ebena* has > 94% survival after four months following 24 hr exposure to air in wet burlap and > 90% survival when in air for 48 hr (Dunn and Layzer, 1996). Incidentally, that study also showed that mussel transport on ice in wet burlap was more harmful than just transport in air with wet burlap. Therefore, transport of specimens in air solely with cool, wet burlap seems to be a feasible method for oxygen-tolerant species.

Some species of mussels can exist in air for days suggesting that they can obtain some oxygen from the air, although at a greatly reduced rate (Hochachka and Guppy, 1987). However, there is a likelihood that ammonia would accumulate in the tissues more during such air exposure because mussels normally excrete this toxic substance through the gills into the water (Withers, 1992). Indeed, this ammonia could contribute to the stress of emersion although there seemingly are no data available on this possibility.

There are several additional factors that might be considered for optimizing the transportation of freshwater mussels. For example, Waller *et al.* (1995) found that *Amblema plicata* (Say, 1817) and *Obliquaria reflexa* (Rafinesque, 1820) had high survival rates after several hours of aerial exposure, when the exposure was conducted in October. However, a trend of decreased survival rate was found when aerial exposure occurred in June. They suggested that these results might be related to the wetness and temperature of the season, thickness of the shell, reproductive status, and level of metabolic activity. *Villosa iris*, a thin-shelled species, was the most sensitive to handling stress in our study, which would make it less able to withstand desiccation than thicker-shelled species (Matteson, 1955; Heming *et al.*, 1988). The effects of ambient temperature are also important, as it was found in pilot studies in our laboratory that *V. iris* has a better ability to regulate its oxygen consumption under hypoxia and is more tolerant of low dissolved oxygen when the temperature was lower (Heath and Chen, 1996). It has also been reported that the survival of mussels after emersion decreases as the relative humidity decreases (Byrne and McMahon, 1991). Finally, since air exposure or hypoxia may cause the release of sperm from males and premature release of embryos or glochidia by females (Waller et al., 1995), the reproductive season may be an inopportune time to transport freshwater mussels, even though glycogen reserves are usually high during that period (Jadhav and Lomte, 1982).

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Current status of freshwater mussels (Unionidae, Margaritiferidae) in the Muscle Shoals area of Tennessee River in Alabama (Muscle Shoals revisited again)

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Abstract: A cumulative total of 79 species of freshwater mussels has been reported from the Tennessee River in the vicinity of Muscle Shoals in northwestern Alabama. This paper documents changes to the fauna during historical times. Sixty-nine species were reported from the area during the early twentieth century, but 32 of those have not been collected since the river was impounded. Twenty of the extirpated species were of Cumberlandian origin. The disappearance of this component of the fauna was accompanied by an invasion of species from downstream. Ten species previously unknown from the Muscle Shoals area have been collected since impoundment of the river. A total of 38 species were collected during recent surveys (1995-1999). Individual accounts are given for all 79 species known from the Muscle Shoals area.

Key Words: Unionidae, recruitment, impoundments

The most diverse freshwater mussel (Bivalvia: Unionoida: Margaritiferidae, Unionidae) fauna ever known was located in the middle reaches of the Tennessee River in northern Alabama (Ortmann, 1924). At a place called Muscle Shoals the river leaves the Highland Rim of the Interior Low Plateau and enters the East Gulf Coastal Plain. Two major freshwater mussel groups, the Cumberlandian and Ohioan, meet at Muscle Shoals (Ortmann, 1924). The Cumberlandian fauna is centered in the upper Tennessee and Cumberland rivers and extends downstream in the Tennessee River to Muscle Shoals, with few elements known to occur downstream of that point (Ortmann, 1925; van der Schalie, 1939). The Ohioan fauna is centered in the Interior Basin, but some of its species range upstream of Muscle Shoals (Ortmann, 1924, 1925; van der Schalie, 1939). Stansbery (1964) considered the Muscle Shoals fauna, prior to impoundment, to consist of 22 Cumberlandian species, 20 Ohioan species and 26 species of unknown origin. Unless otherwise noted, Stansbery's (1964) recognition of Cumberlandian and Ohioan species is used in this paper.

A major factor allowing the great diversity of mussels at Muscle Shoals was the extensive shoal habitat and the presence of numerous large tributaries. Muscle Shoals stretched 53 miles, from (Tennessee River mile) TRM 234.6 to TRM 287.7, and actually encompassed four primary shoal areas: Colbert, Little Muscle, Big Muscle, and Elk River shoals (Isom, 1971). The Muscle Shoals area received much attention from early malacologists. Hinkley (1904) listed mussels collected from the area around the turn of the century. Ortmann (1925) included Muscle Shoals in a thorough study of the mussel fauna below Walden Gorge, Tennessee (TRM 434), incorporating literature and museum records and the results of his own collection efforts. Ortmann reported 69 species, adjusted to current taxonomy (Turgeon *et al.*, 1998). Van der Schalie (1939) reported 39 species from the material of Dr. M. M. Ellis, who surveyed the lower Tennessee River for the U. S. Bureau of Fisheries during 1931, prior to closure of Pickwick and Kentucky dams. Impoundment of the Tennessee River following these early surveys brought about drastic changes to mussel habitat. Subsequent accounts of the Muscle Shoals fauna (Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993) documented ensuing faunal changes. This paper includes up to date species accounts, with comparisons to previous surveys (Table 1).

METHODS

Recent survey work was performed by Alabama Division of Wildlife and Freshwater Fisheries and

Table 1. Comparison of various surveys of middle reaches of Tennessee River in Alabama (TRM 226 to TRM 349). Taxonomy of Turgeon *et al.* (1998) used.

Species	pre-1925[1]	1931[2]	1956-1957[3]	1963-1964[4]	1976-1978[5]	1991[6]	1995-1999[7]
Actinonaias ligamentina	X	X		X			
A. pectorosa	X						
Amblema plicata	X	X	X	X	X	X	X
Anodonta suborbiculata				X	X	X	X
Arcidens confragosus							X
Cumberlandia monodonta	X	X					X
Cyclonaias tuberculata	X	X	X	X	X	X	X
Cyprogenia stegaria [e]	X	X		X	X		
Dromus dromas [e]	X	X					
Ellipsaria lineolata	X	X	X	X	X	X	X
Elliptio crassidens	X	X	X	X	X	X	X
E. dilatata	X	X	X	X	X		X
Epioblasma arcaeformis [x]	X						
E. biemarginata [x]	X						
E. brevidens [e]	X						
E. capsaeformis [e]	X						
E. f. florentina [e, x]	X						
E. haysiana [x]	X						
E. o. obliquata [e, x]	X						
E. personata [x]	X						
E. propinqua [x]	X						
E. t. torulosa [e, x]	X	X					
E. triquetra	X	X					
E. turgidula [e, x]	X						
Fusconaia barnesiana	X						
F. cor [e]	X						
F. cuneolus [e]	X						
F. ebena	X	X		X	X		X
F. subrotunda	X	X		X			X
Hemistena lata [e]	X						
Lampsilis abrupta [e]	X	X		X	X	X	X
L. fasciola	X	X					
L. ovata	X	X		X	X		X
L. teres	X	X		X	X	X	X
L. virescens [e]	X						
Lasmigona complanata					X	X	X
L. costata	X						
Lemiox rimosus [e]	X						
Leptodea fragilis	X	X		X	X	X	X
L. leptodon	X						
Lexingtonia dolabelloides	X	X		X			
Ligumia recta	X	X		X	X		X
Medionidus conradicus	X						
Megalonaias nervosa	X	X	X	X	X	X	X
Obliquaria reflexa	X	X	X	X	X	X	X
Obovaria olivaria	X	X	X	X			
O. retusa [e]	X	X					X
Plethobasus cicatricosus [e]				X			X
P. cooperianus [e]			X	X	X		
P. cyphyus	X	X	X	X	X		X
Pleurobema clava [e]	X						
P. sintoxia	X	X			X		
P. cordatum	X	X	X	X	X	X	X
P. oviforme	X			X	X		
P. plenum [e]	X	X					X
P. rubrum	X	X			X		X

Continued

Table 1. (Continued)

Species	pre-1925[1]	1931[2]	1956-1957[3]	1963-1964[4]	1976-1978[5]	1991[6]	1995-1999[7]
Potamilus alatus	X	X	X	X	X	X	X
P. ohiensis							X
Ptychobranchus fasciolaris	X	X	X	X			X
P. subtentum	X						
Pyganodon grandis				X	X	X	X
Quadrula apiculata							X
Q. c. cylindrica	X	X					
Q. fragosa [e]	X		X				
Q. intermedia [e]	X						
Q. metanevra	X	X	X	X	X		X
Q. p. pustulosa	X	X	X	X	X	X	X
Q. quadrula	X	X		X	X	X	X
Strophitus undulatus	X	X					
Toxolasma lividus					X		X
T. parvus	X				X		X
Tritogonia verrucosa	X	X	X	X	X	X	X
Truncilla donaciformis	X	X	X		X	X	X
T. truncata	X	X					X
Utterbackia imbecillis					X		X
Villosa iris	X						
V. taeniata	X						
V. trabalis [e]	X						
V. v. vanuxemensis	X						X
Totals	69	39	18	32	32	18	39

[e], federally listed as endangered,
[x], possibly extinct according to Turgeon *et al.* (1998).
[1] Ortmann, 1925
[2] van der Schalie, 1939
[3] Scruggs, 1960
[4] Stansbery, 1964 and Isom, 1969
[5] Gooch *et al.*, 1979
[6] Ahlstedt and McDonough, 1993
[7] recent surveys, *O. retusa* record T. Richardson (University of North Alabama, pers. comm.)

Geological Survey of Alabama. From 1995 through 1999 distribution and abundance data were taken from all mussel related activities performed in the study area. Sampling techniques included qualitative searches, quantitative sampling using 0.25 m^2 quadrats and catch per unit effort (C.P.U.E.) sampling. Most dives were performed using surface air supply from a boat, but SCUBA was occasionally used. A total of 253.2 hours of bottom time was spent searching for mussels. Some observations of species from overbank habitat were recorded while walking shorelines during periods of low water levels. Quantitative data were collected for specific reaches and are not presented here. Anecdotal information dealing with commercial mussel harvest discussed in this paper is from receipts completed by mussel buyers during shell transactions.

Subjective abundance information is presented for the current status of each species. Categories include abundant, common, uncommon, rare, and very rare. A species was considered abundant if ten specimens could generally be collected from appropriate habitat with little effort (*i. e.* one hour or less bottom time while diving with surface air supply or SCUBA). Common species were those in which ten specimens could be collected in one day from appropriate habitat, but more effort was required (*i. e.* more than one hour of bottom time). A species was considered uncommon if it was encountered on most days of field work, but ten specimens were usually not encountered during a day. Rare species were those encountered most years, but not collected on most days. Very rare species were those that were not encountered every year. These categories refer to areas in general (*e. g.* Wilson Dam tailwaters). Abundance of a given species generally varied within areas. In tailwater habitat mussels tended to be more abundant toward channel edges than at mid-channel. In reservoir habitat mussel densities were less predictable, but tended to be higher on tops of submerged mounds on overbanks and on channel slopes.

Study Area

Mussel populations have been redistributed in the

Muscle Shoals area due to changes in habitat brought about by construction of Tennessee Valley Authority dams on the Tennessee River at TRM 207 (Pickwick Landing, closed in 1938), TRM 259 (Wilson, closed in 1924), TRM 275 (Wheeler, closed in 1936) and TRM 349 (Guntersville, closed in 1939) (Fig. 1). In Alabama, riverine habitat within the study area is now found only in the tailwaters of these dams. Over 40 miles of riverine habitat exist between Guntersville Dam and the city of Decatur (TRM 306). Therefore, the scope of this work covered areas upstream of the original Muscle Shoals, to Guntersville Dam. Overbank habitat at selected sites on Wheeler and Pickwick reservoirs was surveyed and included in this paper.

For discussion of recent survey work, the study area was divided into four reaches: Pickwick Reservoir, Wilson tailwaters, Wheeler Reservoir, and Guntersville tailwaters. Pickwick Reservoir refers to the river between the mouth of Bear Creek (TRM 226, the downstream extent of survey work) and the lower end of Sevenmile Island complex (TRM 247). The area from the lower end of Sevenmile Island complex upstream to Wilson Dam was considered Wilson tailwaters. Decatur was considered the dividing point between Wheeler Reservoir and Guntersville tailwaters. Most work in Pickwick and Wheeler reservoirs took place on the overbanks, with occasional spot searches of the channel and channel slopes. Wilson Reservoir is small and deep, with little riverine or overbank habitats, relative to Wheeler and Pickwick reservoirs. Though some recent survey work has been performed on Wilson Reservoir, it has not received the attention of the other two and was not addressed in this paper.

Lotic habitat in Wilson and Guntersville tailwaters comprised mostly silt-free bedrock, cobble, gravel, sand, and clay. Immediately below the dams, substrata were mostly bedrock and cobble. Smaller sized particles were more abundant downstream. In lower reaches of tailwaters, substrata downstream of islands and along some shorelines were composed of mostly sand and clay. River discharge was highly variable, being influenced by water release from the dams. Daily water level fluctuations occurred, with flows ranging from imperceptible to swift. Periods of swift water took place each day. Turbidity was typically low in tailwaters, relative to reservoirs. Visibility in the tailwaters was usually 1-3 m.

Pickwick and Wheeler reservoir habitat comprised expanses of lentic overbank with old river channels coursing through them. Habitat was generally muddy and turbid with sluggish current. Substrata were composed of gravel, *Corbicula fluminea* (Müller, 1774) shells, sand, clay, and mud. Silt accumulation varied, depending on current and wave action. Gravel and/or *C. fluminea* shells were generally found on tops of submerged mounds and along some shorelines. Silt accumulation, generally 5-20 mm, was lower in those areas than in deeper water, presumably kept clear by wave action. In deeper water between submerged mounds and in parts of the old channel, silt accumulation was often in excess of 30 cm. Muddy substrata of Pickwick Reservoir were often more sandy than those of Wheeler Reservoir. Submerged tree stumps and snags were common in both reservoirs. Drastic changes in river discharge were not observed in reservoir habitat, with current at most barely perceptible. Visibility in reservoirs was rarely over 1 m and there was often no visibility.

SPECIES ACCOUNTS

Actinonaias ligamentina (Lamarck, 1819) (Mucket)

Ortmann (1925) and van der Schalie (1939) reported *Actinonaias ligamentina gibba* (Simpson, 1900) from Muscle Shoals. The *gibba* subspecies is no longer recognized (Parmalee and Bogan, 1998; Turgeon *et al.*, 1998). Isom (1969) reported a density of 0.012/m^2 for *A. ligamentina* in Guntersville tailwaters in 1963. In a survey of commercial mussel harvest, Bowen *et al.* (1994) observed *A. ligamentina* collected from Wheeler Reservoir by commercial mussel harvesters, though it made up a very small percentage of the harvest. No *A. ligamentina* were encountered during recent surveys. Williams *et al.* (1993) considered this species to be currently stable overall.

Actinonaias pectorosa (Conrad, 1834) (Pheasantshell)

Actinonaias pectorosa was reported from Muscle Shoals by Ortmann (1925), but apparently disappeared soon after impoundment of the river. This Cumberlandian species did not appear in subsequent accounts and was not collected during recent surveys. Williams *et al.* (1993) considered *A. pectorosa* to be of special concern.

Amblema plicata (Say, 1817) (Threeridge)

Amblema plicata was widespread in the study area prior to impoundment (Ortmann, 1925; van der Schalie, 1939). Ortmann (1925) found this species to be abundant from Muscle Shoals upstream, but reported only a single specimen downstream of Muscle Shoals at Dixie (TRM 102). *A. plicata* has fared well with impoundment of the river and appeared in most subsequent accounts of the study area (Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). During recent surveys it was common to abundant in Pickwick Reservoir, common in Wilson tailwaters, uncommon to common in Guntersville tailwaters (abundance increased with an upstream progression) and uncommon in Wheeler Reservoir. Subadults were common in all reaches of the

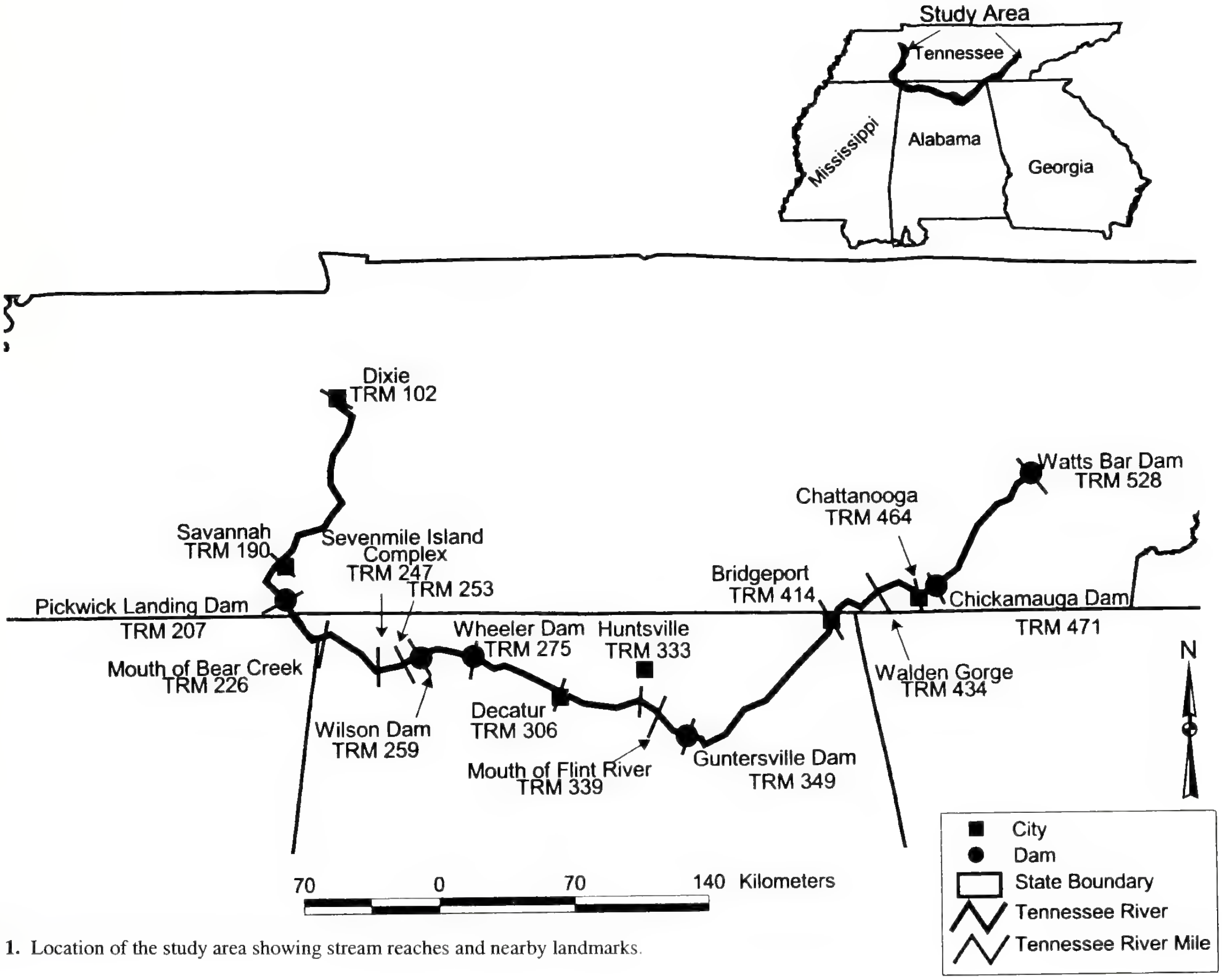
Study Area
Tennessee
Mississippi
Alabama
Georgia
Dixie
TRM 102
Savannah
TRM 190
Sevenmile Island Complex
TRM 247
TRM 253
Pickwick Landing Dam
TRM 207
Mouth of Bear Creek
TRM 226
Wilson Dam
TRM 259
Wheeler Dam
TRM 275
Huntsville
TRM 333
Decatur
TRM 306
Mouth of Flint River
TRM 339
Guntersville Dam
TRM 349
Bridgeport
TRM 414
Chattanooga
TRM 464
Walden Gorge
TRM 434
Chickamauga Dam
TRM 471
Watts Bar Dam
TRM 528
N
70 0 70 140 Kilometers
■ City
● Dam
State Boundary
Tennessee River
Tennessee River Mile

Fig. 1. Location of the study area showing stream reaches and nearby landmarks.

study area except Wheeler Reservoir and lower Guntersville tailwaters. *A. plicata* is currently an important commercial species in Alabama, having comprised 3-13% of the annual reported statewide harvest between 1995 and 1998 (unpublished data). Williams *et al.* (1993) considered this species to be currently stable.

Anodonta suborbiculata Say, 1831 (Flat Floater)

Anodonta suborbiculata, a member of the Ohioan fauna, appears to be a relatively recent invader to the Tennessee River in Alabama. Stansbery (1964) reported it for the first time and it has appeared in most subsequent treatments of the study area (Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). In recent surveys *A. suborbiculata* was uncommon in Pickwick and Wheeler reservoirs. However, fresh dead shells were common on mudflats and exposed shorelines of both reservoirs during periods of low water. This suggests that *A. suborbiculata* was more abundant in shallow water, where limited survey work was performed. Therefore, it was assigned a status of common in Pickwick and Wheeler reservoirs. Williams *et al.* (1993) considered this species to be currently stable.

Arcidens confragosus (Say, 1829) (Rock Pocketbook)

Arcidens confragosus appears to be a relatively recent invader to the middle reaches of the Tennessee River. It did not appear in previous literary accounts of the study area. However, during recent surveys it was found to be common in both Pickwick Reservoir and Wilson tailwaters. Subadults were uncommon in both reaches. Williams *et al.* (1993) considered this species to be currently stable.

Cumberlandia monodonta (Say, 1829) (Spectaclecase)

The only site where Ortmann (1925) reported *Cumberlandia monodonta* from the main stem Tennessee River was at Muscle Shoals, where "a considerable number" of dead shells was found. It was also reported from Muscle Shoals by van der Schalie (1939). Gooch *et al.*

(1979) reported *C. monodonta* as "collected infrequently" from Pickwick Reservoir. Ahlstedt and McDonough (1993) collected relic shells of *C. monodonta* from Wheeler Reservoir, where they listed it as a nonreproducing riverine species. Bowen *et al.* (1994) also reported it from Wheeler Reservoir in very small numbers during a survey of mussel harvest activities. During recent surveys, *C. monodonta* was present, but very rare, in Wilson and Guntersville tailwaters. Williams *et al.* (1993) considered this species to be threatened.

***Cyclonaias tuberculata* (Rafinesque, 1820) (Purple Wartyback)**

Ortmann (1925) reported both typical *Cyclonaias tuberculata* and *C. tuberculata granifera* from Muscle Shoals, where shell morphology of the two forms intergraded. Van der Schalie (1939) reported only *C. tuberculata granifera*. The *granifera* subspecies is no longer recognized (Parmalee and Bogan, 1998; Turgeon *et al.*, 1998). *C. tuberculata* appeared in most subsequent accounts of the study area (Ortmann, 1925; Van der Schalie, 1939; Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979, Ahlstedt and McDonough, 1993). During recent surveys, this species was abundant throughout Wilson tailwaters and in much of the Guntersville tailwaters, uncommon in Pickwick Reservoir and rare in Wheeler Reservoir. Subadults were common to abundant in many tailwater areas. Williams *et al.* (1993) considered this species to be of special concern overall.

***Cyprogenia stegaria* (Rafinesque, 1820) (Fanshell)**

Cyprogenia stegaria appeared in most accounts of the Muscle Shoals fauna (Ortmann, 1925; van der Schalie, 1939; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979). Isom (1969) estimated the density of *C. stegaria* in Guntersville tailwaters as 0.045/m^2 in 1963. Ahlstedt and McDonough (1993) reported only relic specimens. None were collected during recent surveys in the study area, although *C. stegaria* was collected during recent work below Pickwick Dam (personal observation). This species is currently listed as endangered under the federal Endangered Species Act and was also considered endangered by Williams *et al.* (1993).

***Dromus dromas* (Lea, 1834) (Dromedary Pearlymussel)**

Dromus dromas was one of the most abundant species found in aboriginal shell middens by Morrison (1942). However, it apparently disappeared from the study area soon after impoundment of the river. It was reported by Hinkley (1904), Ortmann (1925) and van der Schalie (1939), but is absent from subsequent accounts and was not encountered during recent surveys. This Cumberlandian species is currently listed as endangered under the federal Endangered Species Act and was also considered endangered by Williams *et al.* (1993).

***Ellipsaria lineolata* (Rafinesque, 1820) (Butterfly)**

Ellipsaria lineolata appeared in most accounts of the study area (Ortmann, 1925; van der Schalie, 1939; Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). In recent surveys, it was common in Wilson and Guntersville tailwaters and rare in Pickwick and Wheeler reservoirs. Subadults were uncommon to common in tailwaters. This species is harvested commercially, but currently makes up a very small percentage of the annual statewide harvest (0-2% between 1995 and 1998, unpublished data). Williams *et al.* (1993) considered this Ohioan species to be of special concern.

***Elliptio crassidens* (Lamarck, 1819) (Elephantear)**

Elliptio crassidens appeared in most treatments of the Muscle Shoals fauna (Hinkley, 1904; Ortmann, 1925; van der Schalie, 1939; Stansbery, 1964; Isom, 1969; Gooch et al., 1979; Ahlstedt and McDonough, 1993). During recent surveys it was abundant in Guntersville tailwaters and common to abundant in Wilson tailwaters. *E. crassidens* was rare to uncommon in upper Pickwick and Wheeler reservoirs, most often found associated with the old river channel in those areas, but occasionally encountered on overbanks. Subadults were common in tailwaters. *E. crassidens* has assumed the position of dominant species in Guntersville tailwaters (*e. g.* 70% of five C.P.U.E. samples at TRM 330 in 1997, unpublished data) since Scruggs (1960) reported it making up only 5.8% of bottom samples between TRM 308 and TRM 316 in 1957. Williams *et al.* (1993) considered this species to be currently stable.

***Elliptio dilatata* (Rafinesque, 1820) (Spike)**

Elliptio dilatata appeared in most treatments of the Muscle Shoals fauna (Hinkley, 1904; Ortmann, 1925; van der Schalie, 1939; Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979). Ahlstedt and McDonough (1993) listed it as a nonreproducing riverine species. During recent surveys it was uncommon in Wilson tailwaters and rare in Guntersville tailwaters. No evidence of recent recruitment of this species was observed. Williams *et al.* (1993) considered it to be currently stable overall.

***Epioblasma arcaeformis* (Lea, 1831) (Sugarspoon)**

Ortmann (1925) viewed a record of *Epioblasma arcaeformis* from Muscle Shoals with skepticism. However, Morrison (1942) found it to be widespread and common in aboriginal shell middens in the vicinity of Muscle Shoals. Stansbery (1964) recognized Ortmann's record as valid. Museum specimens from Muscle Shoals, collected prior to impoundment, exist in at least five museums (*i. e.* U. S. National Museum, Philadelphia Academy of Natural Sciences, Ohio State University Museum, Museum of Comparative Anatomy and Florida State Museum) (Sherry Bostick, U. S. Geological Survey, pers. comm., 1999). *E. arcaeformis* did not appear in subsequent accounts of the study area and was not collected during recent surveys. This Cumberlandian species was listed as possibly extinct by Williams *et al.* (1993) and Turgeon *et al.* (1998).

***Epioblasma biemarginata* (Lea, 1857) (Angled Riffleshell)**

Ortmann (1925) reported *Epioblasma biemarginata* to be abundant at Muscle Shoals prior to impoundment, but it did not appear in subsequent accounts of the study area. However, Philadelphia Academy of Natural Sciences possesses a specimen with a label indicating that it was collected just west of Florence in 1970 (Sherry Bostick, U. S. Geological Survey, pers. comm., 1999). *E. biemarginata* was not encountered during recent surveys. This Cumberlandian species was listed as possibly extinct by Williams *et al.* (1993) and Turgeon *et al.* (1998).

***Epioblasma brevidens* (Lea, 1831) (Cumberlandian Combshell)**

Ortmann (1925) reported *Epioblasma brevidens* as rare at Muscle Shoals prior to impoundment. It appeared in no subsequent accounts and was not encountered during recent surveys. This Cumberlandian species is currently listed as endangered under the federal Endangered Species Act and was considered endangered by Williams *et al.* (1993).

***Epioblasma capsaeformis* (Lea, 1834) (Oyster Mussel)**

Ortmann (1925) reported *Epioblasma capsaeformis* from Muscle Shoals prior to impoundment. It was not reported in subsequent accounts or collected during recent surveys. This Cumberlandian species is currently listed as endangered under the federal Endangered Species Act and was considered endangered by Williams *et al.* (1993).

***Epioblasma florentina florentina* (Lea, 1857) (Yellow Blossom)**

Ortmann (1925) reported *Epioblasma florentina florentina* from Muscle Shoals prior to impoundment. It was not reported in subsequent accounts or collected during recent surveys. Stansbery (1964) did not include subspecies in his list, but designated *E. florentina* as a Cumberlandian species. *E. f. florentina* is currently listed as endangered under the federal Endangered Species Act, but considered possibly extinct by Williams *et al.* (1993) and Turgeon *et al.* (1998).

***Epioblasma haysiana* (Lea, 1834) (Acornshell)**

Ortmann (1925) reported *Epioblasma haysiana* from Muscle Shoals prior to impoundment, suggesting that it was "rare and local" in the lower Tennessee River. It was not reported in subsequent accounts or encountered during recent surveys. This Cumberlandian species was listed as possibly extinct by Williams *et al.* (1993) and Turgeon *et al.* (1998).

***Epioblasma obliquata obliquata* (Rafinesque, 1820) (Catspaw)**

Ortmann (1925) reported *Epioblasma obliquata obliquata* from Muscle Shoals prior to impoundment. It was not reported in subsequent accounts or collected during recent surveys. Stansbery (1964) did not include subspecies on his list, but designated *E. obliquata* as a Cumberlandian species. This subspecies is currently listed as endangered under the federal Endangered Species Act and considered endangered by Williams *et al.* (1993). However, it was considered possibly extinct by Turgeon *et al.* (1998).

***Epioblasma personata* (Say, 1829) (Round Combshell)**

Ortmann (1925) collected *Epioblasma personata* from Muscle Shoals prior to impoundment. Ortmann (1925) suggested that this member of the Ohioan fauna was one of the rarest mussel species, even prior to mass alteration of habitat. It did not appear in subsequent accounts and was not encountered during recent surveys. *E. personata* was listed as possibly extinct by Williams *et al.* (1993) and Turgeon *et al.* (1998).

***Epioblasma propinqua* (Lea, 1857) (Tennessee Riffleshell)**

Ortmann (1925) reported *Epioblasma propinqua* from Muscle Shoals prior to impoundment. It was not reported in subsequent accounts or collected during recent surveys. This species was considered to be of Cumberlandian origin by Ortmann (1925), but not included in Stansbery (1964). Williams *et al.* (1993) and Turgeon *et al.* (1998) listed it as possibly extinct.

***Epioblasma torulosa torulosa* (Rafinesque, 1820) (Tubercled Blossom)**

Morrison (1942) reported *Epioblasma torulosa torulosa* to be one of the most abundant species collected from aboriginal shell middens in the Muscle Shoals area. Prior to impoundment, Hinkley (1904) reported *E. t. torulosa* from the Tennessee River at Decatur and Ortmann (1925) and van der Schalie (1939) added records from Muscle Shoals. Van der Schalie (1939) also reported it from the mouth of the Flint River. *E. t. torulosa* was not reported in subsequent accounts or collected during recent surveys. This subspecies is currently listed as endangered under the federal Endangered Species Act, but considered possibly extinct by Williams *et al.* (1993) and Turgeon *et al.* (1998).

***Epioblasma triquetra* (Rafinesque, 1820) (Snuffbox)**

Ortmann (1925) and van der Schalie (1939) reported *Epioblasma triquetra* from Muscle Shoals and Bridgeport (TRM 414) prior to impoundment. Van der Schalie (1939) also examined a specimen from near the mouth of the Flint River. *E. triquetra* did not appear in subsequent accounts and was not collected during recent surveys. Williams *et al.* (1993) considered this species to be threatened.

***Epioblasma turgidula* (Lea, 1858) (Turgid Blossom)**

Ortmann (1925) reported *Epioblasma turgidula* from Muscle Shoals prior to impoundment. It was not reported in subsequent accounts or collected during recent surveys. This Cumberlandian species is currently listed as endangered under the federal Endangered Species Act, but considered possibly extinct by Williams *et al.* (1993) and Turgeon *et al.* (1998).

***Fusconaia barnesiana* (Lea, 1838) (Tennessee Pigtoe)**

Ortmann (1925) reported both typical *Fusconaia barnesiana* and *F. barnesiana tumescens* from Muscle Shoals. The *tumescens* subspecies is no longer recognized (Turgeon *et al.*, 1998). *F. barnesiana* was widespread, in the main river and "all" tributaries, and was apparently common prior to the alteration of shoal habitat (Ortmann, 1925). This Cumberlandian species was not reported in subsequent literature. However, a small number of *F. barnesiana* survived in Wilson tailwaters until at least 1966, when two specimens were collected live (University of North Alabama collection). No *F. barnesiana* were collected during recent surveys. Williams *et al.* (1993) considered this species to be of special concern.

***Fusconaia cor* (Conrad, 1834) (Shiny Pigtoe)**

Fusconaia cor was reported from Muscle Shoals by Ortmann (1925), but not in subsequent literature. However, small numbers of *F. cor* survived in Wilson Dam tailwaters until at least 1968. One live specimen was collected in 1966 and three in 1968 (University of North Alabama collection). *F. cor* was not encountered during recent surveys. This Cumberlandian species is currently listed as endangered under the federal Endangered Species Act. Williams *et al.* (1993) considered this species to be endangered.

***Fusconaia cuneolus* (Lea, 1840) (Finerayed Pigtoe)**

Fusconaia cuneolus was reported from Muscle Shoals by Ortmann (1925) as *F. cuneolus appressa* (Lea, 1871), with Muscle Shoals as the type locality. The subspecies is no longer recognized (Turgeon *et al.*, 1998). *F. cuneolus* appears to have disappeared soon after impoundment of the river and was not reported in subsequent accounts or collected in recent surveys. This Cumberlandian species is currently listed as endangered under the federal Endangered Species Act. Williams *et al.* (1993) considered this species to be endangered.

***Fusconaia ebena* (Lea, 1831) (Ebonyshell)**

The range of *Fusconaia ebena* in the Tennessee River was largely confined to the lower reaches prior to modern habitat alterations. It was not collected from aboriginal shell middens in the vicinity of Muscle Shoals by Morrison (1942), or Chickamauga Reservoir by Parmalee *et al.* (1982). Hinkley (1904) reported *F. ebena* from Decatur, which was the upstream limit of the species prior to impoundment. Ortmann (1925) reported only one specimen of *F. ebena* collected from Muscle Shoals prior to impoundment, though he found it to be more abundant downstream at Dixie. Ortmann (1925) dismissed early records of *F. ebena* from Holston and French Broad rivers (Boepple and Coker, 1912) as misidentifications of *F. subrotunda*. Since Ortmann's (1925) investigation, *F. ebena* has expanded its range upstream to at least Chickamauga Dam (TRM 471), but has not been reported to be common upstream of Wilson Dam (van der Schalie, 1939; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979). During recent surveys, *F. ebena* was abundant in Wilson tailwaters, uncommon to common in Pickwick Reservoir, rare in Guntersville tailwaters and very rare in Wheeler Reservoir. It was the dominant species in Wilson tailwaters (*e. g.* 43% of mussels in five C.P.U.E. samples from TRM 249 in 1997, unpub. data). Recruitment appeared excellent in Wilson tailwaters, with subadults abundant (*e. g.* specimens 1-5 years of age comprised 54% and specimens 6-10 years of age comprised 32% of *F. ebena* in C.P.U.E. samples from TRM 249 in 1997, unpub. data). Subadults were uncommon in Pickwick Reservoir. This species is currently one of the most important commercial mussel species in Alabama, having comprised 24-82% of the annual statewide harvest between 1995 and 1998 (unpub. data). Williams *et al.* (1993) considered this species to be currently stable.

***Fusconaia subrotunda* (Lea, 1831) (Longsolid)**

Fusconaia subrotunda appeared in most accounts of the study area (Ortmann, 1925: van der Schalie, 1939; Stansbery, 1964; Isom, 1969 and Gooch *et al.*, 1979). During recent surveys *F. subrotunda* was found to be a rare species in Wilson tailwaters. Williams *et al.* (1993) considered this species to be of special concern.

Hemistena lata (Rafinesque, 1820) (Cracking Pearlymussel)

Hemistena lata did not fare well with alteration of shoal habitat in the study area. Ortmann (1925) reported it from Muscle Shoals prior to impoundment, but it did not appear in subsequent literature and was not encountered during recent surveys. However, a fresh dead specimen was collected from Elk River in 1999, just upstream of the reach of river impounded by Wheeler Dam (Elk River mile 31.2, Limestone County, Alabama). This species is currently listed as endangered under the federal Endangered Species Act and was considered endangered by Williams *et al.* (1993).

Lampsilis abrupta (Say, 1831) (Pink Mucket)

Hinkley (1904) and Ortmann (1925) reported *Lampsilis abrupta* from Decatur and Muscle Shoals prior to impoundment. Van der Schalie (1939) reported it from two additional sites in the vicinity of Huntsville (TRM 333). It survived habitat alteration and appeared in subsequent accounts (Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). Gooch *et al.* (1979) reported *L. abrupta* as "relatively rare" in Pickwick and Wheeler reservoirs, though they suggested that it was more common in Wheeler Reservoir than elsewhere in the Tennessee River. During recent surveys, *L. abrupta* was uncommon to rare in Wilson and Guntersville tailwaters. Specimens younger than ten years of age were rarely encountered in either reach. This species is currently listed as endangered under the federal Endangered Species Act and was considered endangered by Williams *et al.* (1993).

Lampsilis fasciola Rafinesque, 1820 (Wavyrayed Lampmussel)

Ortmann (1925) and van der Schalie (1939) reported *Lampsilis fasciola* from Muscle Shoals. It was last reported as "collected infrequently" by Gooch *et al.* (1979) and has not been encountered in recent surveys. Williams *et al.* (1993) considered this species to be currently stable.

Lampsilis ovata (Say, 1817) (Pocketbook)

Lampsilis ovata was reported from Tennessee River sites across north Alabama both before and after impoundment (Ortmann, 1925; van der Schalie, 1939; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979). Ahlstedt and McDonough (1993) listed it as a nonreproducing riverine species in Wheeler Reservoir and Guntersville tailwaters. During recent surveys, *L. ovata* was collected only from Wilson tailwaters, where occasional specimens as young as three years of age were encountered. Williams *et al.* (1993) considered this species to be of special concern.

Lampsilis teres (Rafinesque, 1820) (Yellow Sandshell)

Lampsilis teres appeared in most accounts of the study area (Ortmann, 1925; van der Schalie, 1939; Stansbery; 1964, Isom; 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). Though uncommonly collected during dive surveys of all reaches in the study area, fresh dead shells of *L. teres* were common on mudflats and shores of many areas. This may be a reflection of this species' tendency to remain burrowed deeply in the substratum for much of the year (personal observation). Williams *et al.* (1993) considered this species to be currently stable.

Lampsilis virescens (Lea, 1858) (Alabama Lampmussel)

Muscle Shoals was the only main stem Tennessee River site from which Ortmann (1925) reported *Lampsilis virescens*. It was not reported in subsequent accounts or collected during recent surveys. This Cumberlandian species is currently listed as endangered under the federal Endangered Species Act and was considered endangered by Williams *et al.* (1993).

Lasmigona complanata complanata (Barnes, 1823) (White Heelsplitter)

Lasmigona complanata complanata appears to be a relatively recent invader of the study area. It was not reported from Muscle Shoals prior to impoundment. Ortmann (1925) collected it from the lower Duck River and stated that it occurred nowhere else in the Tennessee drainage. However, the distribution map of Parmalee and Bogan (1998) showed *L. c. complanata* to be widely distributed in the upper Tennessee River system, though no dates for those collections were given. Gooch *et al.* (1979) reported *L. c. complanata* from Spring Creek embayment of Wheeler Reservoir, near TRM 283.8, and Ahlstedt and McDonough (1993) reported it from Guntersville tailwaters. During recent surveys it was found to be a rare species in Guntersville tailwaters and Wheeler Reservoir. Williams *et al.* (1993) considered this species to be currently stable.

Lasmigona costata (Rafinesque, 1820) (Flutedshell)

Ortmann (1925) reported *Lampsilis costata* to be rare in the main stem Tennessee River. It did not appear in subsequent accounts and was not collected during recent surveys. Williams *et al.* (1993) considered this species to be currently stable.

Lemiox rimosus (Rafinesque, 1831) (Birdwing Pearlymussel)

Lemiox rimosus was reported from Muscle Shoals by Ortmann (1925). It did not appear in subsequent literature and was not collected during recent surveys. This Cumberlandian species is currently listed as endangered under the federal Endangered Species Act and was considered endangered by Williams *et al.* (1993).

***Leptodea fragilis* (Rafinesque, 1820) (Fragile Papershell)**

Leptodea fragilis was included in most accounts of the Muscle Shoals fauna (Ortmann, 1925; van der Schalie, 1939; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). During recent surveys, *L. fragilis* was common in Pickwick Reservoir and Wilson tailwaters and uncommon in Wheeler Reservoir and Guntersville tailwaters. Subadults were uncommon in Pickwick Reservoir and Wilson tailwaters. Williams *et al.* (1993) considered this species to be currently stable.

***Leptodea leptodon* (Rafinesque, 1820) (Scaleshell)**

Leptodea leptodon was reported from Muscle Shoals by Ortmann (1925), but has not appeared in subsequent treatments or been encountered in recent surveys. Williams *et al.* (1993) considered this species to be endangered.

***Lexingtonia dolabelloides* (Lea, 1840) (Slabside Pearlymussel)**

Ortmann (1925) reported only the typical form of *Lexingtonia dolabelloides* from Muscle Shoals. However, van der Schalie (1939) reported both the typical form and *L. dolabelloides conradi*, which was considered the headwaters subspecies. The *conradi* subspecies is no longer recognized (Turgeon *et al.*, 1998). Stansbery (1964) also collected *L. dolabelloides*, though Ortmann's (1925) record was omitted from that account. It did not appear in subsequent accounts, but a single specimen collected from Wilson tailwaters in 1966 is in the University of North Alabama (UNA) collection. This species was not encountered in recent surveys. Ortmann (1925) considered *L. dolabelloides* to be a Cumberlandian species, but Stansbery (1964) listed it as an Ohioan species. Williams *et al.* (1993) considered this species to be threatened.

***Ligumia recta* (Lamarck, 1819) (Black Sandshell)**

Ligumia recta appeared in most accounts of the study area (Ortmann, 1925, van der Schalie, 1939, Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979). Ahlstedt and McDonough (1993) reported the population of *L. recta* in Guntersville tailwaters to be nonreproducing. During recent surveys it was rare in Guntersville tailwaters and uncommon in Wilson tailwaters. Occasional *L. recta* as young as four years of age were collected from Wilson tailwaters, but all from Guntersville tailwaters were mature. Williams *et al.* (1993) considered this species to be special concern.

***Medionidus conradicus* (Lea, 1834) (Cumberland Moccasinshell)**

Medionidus conradicus apparently disappeared from the study area soon after destruction of the shoal habitat. This Cumberlandian species was reported by Ortmann (1925), but was not found in subsequent accounts or collected during recent surveys. Williams *et al.* (1993) considered this species to be of special concern.

***Megalonaias nervosa* (Rafinesque, 1820) (Washboard)**

Ortmann (1925) reported *Megalonaias nervosa* from Muscle Shoals, but stated that it was scarce upstream of Dixie, where it was "very abundant." It appeared in most subsequent accounts of the study area (van der Schalie, 1939; Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). *M. nervosa* has thrived with impoundment of the river and advanced upstream to at least Watts Bar Dam tailwaters (TRM 528) (Ahlstedt and McDonough, 1995-1996). During recent surveys it was found to be common in both riverine and overbank habitat throughout the study area and was the dominant species in many areas of Wheeler Reservoir (*e. g.* 72% of mussels in ten C.P.U.E. samples from TRM 292 in 1997, unpublished data). Subadults were uncommon in all reaches. *M. nervosa* is currently one of the most important commercial mussel species harvested in Alabama. It comprised 45% of mussels harvested during a survey of commercial mussel harvesters in 1991 and 1992 (Bowen *et al.*, 1994) and 6-46% of the annual statewide harvest from 1995 through 1998 (unpub. data). Williams *et al.* (1993) considered this species to be of special concern.

***Obliquaria reflexa* (Rafinesque, 1820) (Threehorn Wartyback)**

This species appeared in most accounts of the study area (Ortmann, 1925; van der Schalie, 1939; Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). During recent surveys, it was abundant in Wilson tailwaters, common to abundant in Guntersville tailwaters and common in Pickwick and Wheeler reservoirs. Subadults were common in tailwaters and uncommon in reservoirs. However, subadults may have been more abundant in reservoirs, but difficult to find due to their small size and poor visibility in that habitat. Williams *et al.* (1993) considered this species to be currently stable.

***Obovaria olivaria* (Rafinesque, 1820) (Hickorynut)**

This species appeared in most accounts of the Muscle Shoals fauna (Ortmann, 1925; van der Schalie, 1939; Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979). According to Ortmann (1925) Muscle Shoals was the upstream limit of *Obovaria olivaria* in the Tennessee system. Gooch *et al.* (1979) reported it to be "collected infrequently" in Pickwick Reservoir. However, it was not collected during recent surveys. Williams *et al.* (1993) considered this species to be currently stable.

Obovaria retusa (Lamarck, 1819) (Ring Pink)

Obovaria retusa was reported from Decatur by Hinkley (1904) and Muscle Shoals by Ortmann (1925) and van der Schalie (1939), but did not appear in subsequent accounts. However, a single specimen was collected from Wilson tailwaters by a commercial mussel harvester in 1992 and identified by Dr. Terry Richardson (UNA, personal communication, 1992). The status of very rare has been assigned to *O. retusa* based on this record. This species is currently listed as endangered under the federal Endangered Species Act, and Williams *et al.* (1993) considered it to be endangered as well.

Plethobasus cicatricosus (Say, 1829) (White Wartyback)

The first report of *Plethobasus cicatricosus* from the middle reaches of the Tennessee River was by Stansbery (1964), who collected it at Muscle Shoals. It did not appear in subsequent accounts. During recent surveys *P. cicatricosus* was rare in Wilson tailwaters, with five specimens collected between 1997 and 1999. Three specimens were relatively recent recruits to the population, ranging in age from three to six years based on external shell annuli counts. One fresh dead specimen was also collected from Wilson tailwaters. This species is currently listed as endangered under the federal Endangered Species Act, and Williams *et al.* (1993) considered it to be endangered as well.

Plethobasus cooperianus (Lea, 1834) (Orangefoot Pimpleback)

Though Ortmann (1925) and van der Schalie (1939) did not report *Plethobasus cooperianus* from Muscle Shoals, they did report it from upstream of the study area at Bridgeport and downstream at Dixie and Savannah (TRM 190). Scruggs (1960) reported *P. cooperianus* from Guntersville tailwaters and Stansbery (1964) reported it from Muscle Shoals. It was reported as "relatively uncommon" in the riverine reaches of Wheeler Reservoir by Gooch *et al.* (1979). No *P. cooperianus* were collected from the study area during recent surveys. However, it was recently collected from riverine habitat below Pickwick Dam (personal observation, 1998). This species is currently listed as endangered under the federal Endangered Species Act, and Williams *et al.* (1993) considered it to be endangered as well.

Plethobasus cyphyus (Rafinesque, 1820) (Sheepnose)

Plethobasus cyphyus was apparently never common in the lower Tennessee River. Ortmann (1925) reported it occurring "sparingly" at Muscle Shoals. It was also reported from Guntersville tailwaters by Scruggs (1960) and Muscle Shoals by Stansbery (1964). Gooch *et al.* (1979) reported *P. cyphyus* as "relatively uncommon" in Wheeler Reservoir. Bowen *et al.* (1994) reported very small numbers of *P. cyphyus* in the possession of mussel harvesters on Wheeler Reservoir. *P. cyphyus* was rare in Wilson tailwaters during recent surveys. One five-year-old individual collected from Wilson tailwaters in 1998 provided evidence of recent recruitment. Two fresh dead specimens were recently collected from Guntersville tailwaters, suggesting that *P. cyphyus* also survives there as a very rare species. Williams *et al.* (1993) considered this species to be threatened.

Pleurobema clava (Lamarck, 1819) (Clubshell)

Ortmann (1925) reported four specimens of *Pleurobema clava* from Muscle Shoals. Though it is a member of the Ohioan fauna, it is generally found in streams smaller than the Tennessee River (Ortmann, 1925). *P. clava* was not reported in subsequent treatments of the study area or collected during recent surveys. This species is currently listed as endangered under the federal Endangered Species Act, and Williams *et al.* (1993) considered it to be endangered as well.

Pleurobema cordatum (Rafinesque, 1820) (Ohio Pigtoe)

Pleurobema cordatum appeared in many accounts of the lower Tennessee River mussel fauna (Hinkley, 1904; Ortmann, 1925; van der Schalie, 1939; Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). It was the most abundant mussel and most important commercial species in Guntersville tailwaters when Scruggs (1960) assessed the population and fishery. *P. cordatum* comprised 52.7% of specimens collected during bottom sampling by Scruggs (1960). Scruggs estimated the density of *P. cordatum* between TRM 308 and TRM 316 to be 2.3/m^2 in 1957, with a total population of 20.6 million. However, this species appears to have had trouble adjusting to impoundment, even in tailwater areas. Scruggs (1960) and Isom (1969) documented cessation of reproduction and decline of *P. cordatum* populations following impoundment. Densities of the species in Guntersville tailwaters had dropped to 0.42 and 0.39/m^2 in 1963 and 1964, respectively (Isom, 1969). Ahlstedt and McDonough (1993) documented further declines of *P. cordatum* in Guntersville tailwaters, reporting a density of 0.05/m^2, with no specimens younger than 21 years of age collected. During recent surveys, *P. cordatum* was common in parts of Guntersville tailwaters and uncommon in Wilson tailwaters. Wherever it was encountered, most of the specimens were old, with no recent recruits collected from Guntersville tailwaters and subadults collected from Wilson tailwaters only rarely. *P. cordatum* are still harvested commercially, though currently make up a small percentage of the annual harvest in Alabama. Between 1995 and 1998 *P. cordatum* comprised only 0.3-5% of the annual statewide harvest (unpublished data). Williams *et al.* (1993) considered this species to be of special concern.

Pleurobema oviforme **(Conrad, 1834) (Tennessee Clubshell)**

Ortmann (1925) reported the "large river form," *Pleurobema oviforme holstonense* (Lea, 1840), from Muscle Shoals. This subspecies is no longer recognized (Turgeon *et al.*, 1998). *P. oviforme* apparently did not fare well with destruction of shoal habitat, but was reported by Stansbery (1964) from Muscle Shoals and by Gooch et al. (1979), from Wheeler Reservoir, where it was "relatively uncommon." One live specimen of this Cumberlandian species was collected from the tailwaters of Pickwick Dam in 1988 (personal observation). Williams *et al.* (1993) considered this species to be of special concern.

Pleurobema plenum **(Lea, 1840) (Rough Pigtoe)**

Pleurobema plenum was reported from Decatur by Hinkley (1904) and Muscle Shoals by Ortmann (1925) and van der Schalie (1939). It did not appear in subsequent accounts of the Muscle Shoals fauna. However, collection of one specimen from Wilson tailwaters in 1999 gave it a status of very rare. This species is currently listed as endangered under the federal Endangered Species Act. Williams *et al.* (1993) considered this species to be endangered.

Pleurobema rubrum **(Rafinesque, 1820) (Pyramid Pigtoe)**

Ortmann (1925) described *Pleurobema rubrum* as "rare" at Muscle Shoals, though both he and van der Schalie (1939) reported it to be widespread in the lower Tennessee River. Gooch *et al.* (1979) reported it from both Pickwick and Wheeler reservoirs, where it was described as "relatively uncommon." During recent surveys it was uncommon in Wilson and Guntersville tailwaters. No evidence of recent recruitment (*i. e.* specimens younger than ten years of age) was encountered in either area. Williams *et al.* (1993) considered this species to be threatened.

Pleurobema sintoxia **(Rafinesque, 1820) (Round Pigtoe)**

Both Ortmann (1925) and van der Schalie (1939) reported *Pleurobema sintoxia* from the study area, but Ortmann described it as "rare." It remained extant in the study area into the 1970s, when Gooch *et al.* (1979) reported it as "relatively uncommon" in Wheeler Reservoir. *P. sintoxia* was not reported in subsequent accounts or collected during recent surveys. Williams *et al.* (1993) considered this species to be currently stable.

Potamilus alatus **(Say, 1817) (Pink Heelsplitter)**

Potamilus alatus appeared in most accounts of the Muscle Shoals fauna (Hinkley, 1904; Ortmann, 1925; van der Schalie, 1939; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). It was common to abundant in all reaches of the study area during recent surveys. Subadults were uncommon throughout the study area. Williams *et al.* (1993) considered this species to be currently stable.

Potamilus ohiensis **(Rafinesque, 1820) (Pink Papershell)**

Ortmann (1925) did not report *Potamilus ohiensis* from the study area, but did observe a specimen from adjacent Flint Creek. Stansbery (1964) was the first to report it from the main stem Tennessee River in Alabama. Live *P. ohiensis* were rare in Pickwick and Wheeler reservoirs during recent surveys. However, fresh dead shells were often found along the shoreline at most locations searched, suggesting that they might be more abundant in shallows that are seldom explored using dive equipment. The status of this species appears to be common in Pickwick Reservoir and uncommon in Wheeler Reservoir, based on the presence of dead shells. Williams *et al.* (1993) considered this species to be currently stable.

Ptychobranchus fasciolaris **(Rafinesque, 1820) (Kidneyshell)**

Ptychobranchus fasciolaris was reported from the study area by Ortmann (1925), van der Schalie (1939) and Stansbery (1964). During recent surveys it was very rare in Wilson tailwaters, with two live specimens collected. However, one specimen was eight years of age as evidenced by counts of external shell annuli, indicating recent recruitment. A weathered dead *P. fasciolaris* was also collected from Guntersville tailwaters, suggesting that it remains a very rare species there as well. Williams *et al.* (1993) considered this species to be currently stable.

Ptychobranchus subtentum **(Say, 1825) (Fluted Kidneyshell)**

Ptychobranchus subtentum was apparently common in the lower Tennessee River prior to impoundment (Ortmann, 1925). However, this Cumberlandian species evidently disappeared soon after the habitat was altered. *P. subtentum* appeared in no subsequent accounts and was not collected during recent surveys. Williams *et al.* (1993) considered this species to be of special concern.

Pyganodon grandis **(Say, 1829) (Giant Floater)**

Pyganodon grandis was first reported from the study area by Stansbery (1964), though Ortmann (1925) reported it from several Tennessee River tributaries. It has spread to overbank habitat in Pickwick and Wheeler reservoirs, where it was common during recent surveys. Subadults were uncommon. Williams *et al.* (1993) considered this species to be currently stable.

Quadrula apiculata **(Say, 1829) (Southern Mapleleaf)**

Quadrula apiculata is a species native to Gulf of Mexico coastal drainages, including the lower Mississippi River system. It was recently introduced into the Tennessee River (Parmalee and Bogan, 1998), where it was common in Pickwick Reservoir and Wilson tailwaters during recent surveys. Williams *et al.* (1993) considered this species to be currently stable.

Quadrula cylindrica cylindrica **(Say, 1817) (Rabbitsfoot)**

Quadrula cylindrica cylindrica was reported from the study area by Ortmann (1925) and van der Schalie (1939). It did not appear in subsequent accounts and was not collected during recent surveys. However, *Q. c. cylindrica* was collected during recent work in Pickwick tailwaters (personal observation, 1998), where it was found primarily on channel slopes and marginal clay/sand shelf. Williams *et al.* (1993) considered this species to be threatened.

Quadrula fragosa **(Conrad, 1835) (Winged Mapleleaf)**

Ortmann (1925) reported *Quadrula quadrula fragosa* from Muscle Shoals. Stansbery (1964) apparently did not recognize the record in his comparison of Ortmann's (1925) historic and current faunas. However, Parmalee and Bogan (1998) evidently recognized the record as valid by placing the trinomen *Q. quadrula fragosa* in the synonymy of *Q. fragosa,* and crediting the combination to Ortmann (1925). Scruggs (1960) used *Q. fragosa* for the "Maple-leaf" in his work on Guntersville tailwaters. Mapleleaf has long been the colloquial name for *Quadrula quadrula* (Rafinesque, 1820) and it is unclear whether the common or scientific name was misrepresented. In any case, *Q. fragosa* appears to be extirpated from the study area since it has not appeared in recent accounts and was not encountered during recent surveys. This species is currently listed as endangered under the federal Endangered Species Act, and Williams *et al.* (1993) considered it to be endangered as well.

Quadrula intermedia **(Conrad, 1836) (Cumberland Monkeyface)**

Ortmann (1925) reported *Quadrula intermedia* from Muscle Shoals, but it apparently disappeared soon after destruction of the shoal habitat. It was not included in subsequent accounts or collected during recent surveys. This Cumberlandian species is currently listed as endangered under the federal Endangered Species Act, and Williams *et al.* (1993) considered it to be endangered as well.

Quadrula metanevra **(Rafinesque, 1820) (Monkeyface)**

Ortmann (1925) reported *Quadrula metanevra* to be "fairly abundant" in the Tennessee River. It also appeared in most subsequent accounts (van der Schalie, 1939; Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). *Q. metanevra* was uncommon in Wilson and Guntersville tailwaters during recent surveys, being slightly more abundant in the latter. Most of the specimens encountered were mature (*i. e.* older than 10 years of age), though occasional younger specimens were collected from both areas. Williams *et al.* (1993) considered this species to be currently stable.

Quadrula pustulosa pustulosa **(Lea, 1831) (Pimpleback)**

Ortmann (1925) found *Quadrula pustulosa pustulosa* to be common in the main river, as well as in tributaries adjacent to the study area. It appeared in most subsequent accounts (van der Schalie, 1939; Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). During recent surveys, *Q. p. pustulosa* was common to abundant in all reaches of the study area. Subadults were common in Pickwick Reservoir and Wilson and Guntersville tailwaters and uncommon in Wheeler Reservoir. Williams *et al.* (1993) considered this species to be currently stable.

Quadrula quadrula **(Rafinesque, 1820) (Mapleleaf)**

Ortmann (1925) did not report *Quadrula quadrula* from Muscle Shoals, but it has appeared in most subsequent treatments of the area's mussel fauna (van der Schalie, 1939; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979; Ahlstedt and McDonough, 1993). During recent surveys *Q. quadrula*, including subadults, were abundant in Pickwick Reservoir and common in Wilson tailwaters, but rare to uncommon in Wheeler Reservoir and rare in Guntersville tailwaters. *Q. quadrula* is currently one of the more important commercial species harvested in Alabama. It comprised 6-17% of the annual statewide harvest between 1995 and 1998 (unpublished data). Williams *et al.* (1993) considered this species to be currently stable.

Strophitus undulatus **(Say, 1817) (Creeper)**

Ortmann (1925) reported *Strophitus undulatus* from Muscle Shoals, though commented on its being more abundant elsewhere in the Interior Basin, as well as in the upper Tennessee River system. *S. undulatus* was also reported from Muscle Shoals by van der Schalie (1939), but did not appear in subsequent accounts and was not collected during recent surveys. Williams *et al.* (1993) considered this species to be currently stable.

Toxolasma lividus **Rafinesque, 1831 (Purple Lilliput)**

Ortmann (1925) did not report *Toxolasma lividus* from the main stem Tennessee River, but did report it from six tributaries adjacent to the study area. It did not appear in subsequent accounts until Gooch *et al.* (1979) reported it from Wheeler Reservoir. Recent surveys have shown *T. lividus* to be uncommon to common in Wilson tailwaters. It was rare to uncommon in Guntersville tailwaters and Pickwick and Wheeler reservoirs. Few subadults of this species were encountered in any reach of the study area, possibly due to their small size. This species was considered to be of Cumberlandian origin by Ortmann (1925). Williams *et al.* (1993) considered this species to be of special concern.

Toxolasma parvus **(Barnes, 1823) (Lilliput)**

Ortmann (1925) mentioned a single specimen of *Toxolasma parvus* from Muscle Shoals, but was skeptical of its origin. Gooch *et al.* (1979) reported *T. parvus* from Wheeler Reservoir. *T. parvus* was rarely found during dive surveys in Wilson tailwaters and Pickwick Reservoir. However, fresh dead shells were common on many shorelines and mudflats of Pickwick Reservoir during periods of low water levels. This suggests that *T. parvus* was overlooked during dive surveys, possibly due to its small size or preference for shallow water. Based on the number of dead specimens, its status in Pickwick Reservoir was upgraded to common. Williams *et al.* (1993) considered this species to be currently stable.

Tritogonia verrucosa **(Rafinesque, 1820) (Pistolgrip)**

Ortmann (1925) indicated that *Tritogenia verrucosa* was abundant throughout the Tennessee River. It appeared in most subsequent accounts of the area's mussel fauna (van der Schalie, 1939; Scruggs, 1960; Stansbery, 1964; Isom, 1969; Gooch *et al.*, 1979 and Ahlstedt and McDonough, 1993). During recent surveys, *T. verrucosa* was uncommon to common throughout the study area. Subadults were uncommon in all reaches except Wheeler Reservoir. Williams *et al.* (1993) considered this species to be currently stable.

Truncilla donaciformis **(Lea, 1828) (Fawnsfoot)**

This species appeared in most treatments of the Muscle Shoals fauna (Ortmann, 1925; van der Schalie, 1939; Scruggs, 1960; Gooch *et al.*, 1979, Ahlstedt and McDonough, 1993). During recent surveys, *Truncilla donaciformis* was common to abundant in Wilson tailwaters and uncommon in Guntersville tailwaters and some areas of Pickwick Reservoir. Subadults were uncommon in all three reaches. Williams *et al.* (1993) considered this species to be currently stable.

Truncilla truncata **Rafinesque, 1820 (Deertoe)**

Ortmann (1925) reported *Truncilla truncata* to be abundant at Muscle Shoals. It was also reported from the area by van der Schalie (1939), but appeared in no subsequent accounts. However, *T. truncata* appears to be making a comeback in the lower Tennessee River and was very rare in Wilson tailwaters during recent surveys. This species was uncommon in Pickwick tailwaters during recent surveys of that area (personal observation, 1999). Williams *et al.* (1993) considered this species to be currently stable.

Utterbackia imbecillis **(Say, 1829) (Paper Pondshell)**

Ortmann (1925) reported *Utterbackia imbecillis* from the Paint Rock River and van der Schalie (1939) reported it from the Tennessee River at Savannah, but it was not reported from the study area until 1978 (Gooch *et al.*, 1979). Though rarely encountered during dive surveys, fresh dead shells were common along shorelines and mudflats during periods of low water levels on Pickwick and Wheeler reservoirs. Williams *et al.* (1993) considered this species to be currently stable.

Villosa iris **(Conrad, 1834) (Rainbow)**

Villosa iris, as currently recognized, is considered a species complex with morphologically similar congeners in the Mobile River system (Parmalee and Bogan, 1998). Until taxonomic revision of the complex is complete, Parmalee and Bogan (1998) chose to include all *V. iris* synonyms described from the Ohio River basin in the *V. iris* complex. Parmalee and Bogan (1998) restricted the use of *V. nebulosa* (Conrad, 1834), which has often been included in treatments from the Ohio River system, to species occurring in the Mobile River drainage. Ortmann (1925) regarded "*V. nebulosa*" as Cumberlandian in origin and *V. iris* as from "the Ohio- and Lakes-drainage." Ortmann (1925) reported "*V. nebulosa*" from Muscle Shoals. This species apparently disappeared from the study area soon after impoundment and did not appear in subsequent accounts or recent surveys. Williams *et al.* (1993) considered this species to be currently stable.

Villosa taeniata **(Conrad, 1834) (Painted Creekshell)**

Villosa taeniata appears to have disappeared from the main stem Tennessee River soon after impoundment. This Cumberlandian species was reported from Muscle Shoals by Ortmann (1925), but was not included in subsequent accounts or collected during recent surveys. Williams *et al.* (1993) considered this species to be currently stable.

***Villosa trabalis* (Conrad, 1834) (Cumberland Bean)**

Ortmann (1925) reported *Villosa trabalis* as rare at Muscle Shoals. This Cumberlandian species did not appear in subsequent accounts and was not encountered during recent surveys. *V. trabalis* is currently listed as endangered under the federal Endangered Species Act, and was considered endangered by Williams *et al.* (1993).

***Villosa vanuxemensis vanuxemensis* (Lea, 1838) (Mountain Creekshell)**

The only site where Ortmann (1925) reported *Villosa vanuxemensis vanuxemensis* in main stem Tennessee River was at Muscle Shoals. This Cumberlandian species did not appear in subsequent accounts of the study area. However, four specimens were collected from Wilson tailwaters during recent surveys, giving it a very rare status for that reach. Williams *et al.* (1993) considered this species to be of special concern.

DISCUSSION

A cumulative total of 79 species is known from the Muscle Shoals area. With impoundment of the Tennessee River, alteration of habitat brought substantial changes to the mussel fauna. Of 69 species known from the study area prior to impoundment, 32 have not been reported since van der Schalie (1939). Twenty-two species from the cumulative list are currently recognized as endangered under the federal Endangered Species Act and nine were listed as possibly extinct by Turgeon *et al.* (1998). Thirty-eight species were collected alive during recent surveys.

In addition to elimination of a number of species from the Muscle Shoals area, a major change in the fauna has been a shift from a community with a large component of Cumberlandian species to one dominated by species of Ohioan or unknown origin. Stansbery (1964) considered 22 species known from Muscle Shoals prior to impoundment to be of Cumberlandian origin. Morrison (1942) collected 53 species, adjusted to the current taxonomy of Turgeon *et al.* (1998), from archaeological digs in the vicinity. Three of the five most abundant species reported by Morrison were Cumberlandian, *Epioblasma t. torulosa, E. propinqua* and *Dromus dromas*, with the remaining two species, *Cyclonaias tuberculata* and *Elliptio dilatata*, being of unknown origin. Only two taxa belonging to the Cumberlandian fauna, *Toxolasma lividus* and *Villosa v. vanuxemensis*, were collected during recent surveys of the main stem Tennessee River.

Elimination of Cumberlandian species from the Muscle Shoals area was accompanied by further invasion of species from downstream. Notably absent from the archaeological record are some of the more common species in the area today, including *Fusconaia ebena, Megalonaias nervosa, Obliquaria reflexa* and *Truncilla donaciformis* (Morrison, 1942). Whether the absence of these species from aboriginal shell middens is due to biased harvest or their scarcity during prehistoric times is unclear. Ten species of Ohioan or unknown origin have been added to the faunal list since impoundment: *Plethobasus cicatricosus, Plethobasus cooperianus, Anodonta suborbiculata, Potamilus alatus, Potamilus ohiensis* and *Pyganodon grandis*, by Stansbery (1964), *Lasmigona complanata*, and *Utterbackia imbecillis* by Gooch *et al.* (1979) and *Arcidens confragosus* and *Quadrula apiculata* during recent surveys. However, *P. cooperianus* and *P. ohiensis* were likely present, but overlooked, in the study area prior to impoundment. *Plethobasus cooperianus* was known from upstream and downstream of the study area and *P. ohiensis* was known from Flint Creek, which is an adjacent tributary (Ortmann, 1925; van der Schalie, 1939). *Plethobasus cicatricosus* is a riverine species which was also likely present, but overlooked, prior to impoundment. *Toxolasma parvus* was reported from Muscle Shoals by Ortmann (1925), but the origin of the single specimen was viewed with skepticism by that author. Thus, it may or may not be a recent invader to the study area. The remaining six species thrive in overbank habitat and appear to have invaded the study area following creation of that environment. *Arcidens confragosus* was found to be doing well in riverine habitat, as well as on overbanks, during recent surveys. Bates (1962) documented mussel invasion of overbank habitat in Kentucky Reservoir fourteen years after impoundment. *Anodonta suborbiculata, P. ohiensis, P. grandis, T. parvus* and *U. imbecillis* were all found to be early invaders, along with *Quadrula quadrula* and *Leptodea fragilis*.

In addition to new invaders, several species have either expanded their ranges upstream and/or increased their relative abundance in the study area. *Fusconaia ebena*, *Megalonaias nervosa* and *Quadrula quadrula*, all considered to be Ohioan in origin by Stansbery (1964), were rare in the study area prior to impoundment (Ortmann, 1925), but have since increased in abundance. During recent work, *F. ebena* and *M. nervosa* were the most abundant species in Wilson tailwaters and Wheeler Reservoir, respectively. *Fusconaia ebena* and *Q. quadrula* were found as far upstream as Guntersville Dam during recent surveys and *M. nervosa* has advanced at least to Watts Bar Dam tailwaters (Ahlstedt and McDonough, 1994). As with most of the recent invaders, *M. nervosa* and *Q. quadrula* do well in overbank habitat. *Fusconaia ebena* is primarily a species of riverine habitat, but also occurs on overbanks. Oddly, one of the remaining Cumberlandian species, *Toxolasma lividus,* appears to have increased in abundance following impoundment of the river, and is now thriving in overbank habitat. With the ability of this species to survive in lentic habitat, which is uncharacteristic of the Cumberlandian fauna in general, and its presence well up into the Ohio River system (Cummings and Mayer, 1992), inclusion of *T. lividus* in the Cumberlandian fauna may warrant reconsideration.

An obvious reason for expansion of Ohioan species in the Tennessee River was creation of favorable overbank habitat. However, changes in fish host distribution and abundance may have also played a role in faunal modifications. In addition to invasion of the river by Ohioan species, construction of the Tennessee-Tombigbee Waterway may have opened a path for emigration of Mobile Basin species. To date, *Quadrula apiculata* is the only Mobile Basin mussel known to have become recently established in the Tennessee River, but it was apparently intentionally released into the river during the 1980's (Parmalee and Bogan, 1998).

Two exotic non-unionid species were collected during recent surveys. *Dreissena polymorpha* (Pallas, 1771), the zebra mussel, was found to be uncommon to common in Wilson and Guntersville tailwaters and rare in Pickwick and Wheeler reservoirs. *Corbicula fluminea* was common to abundant throughout the study area.

Though changes to the middle reaches of the Tennessee River have been severe, the mussel fauna remains diverse and abundant. During recent quantitative studies, mussel densities in Wilson tailwaters were routinely in the range of 40/m^2 (unpub. data). Mussel populations appear to have stabilized since impoundment. However, continued vigilance will be required to prevent further depletion of the fauna. With recent advances in mussel propagation technology and improvements in water quality, reintroductions of historic elements may be possible in the near future.

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Larval and Post-larval Shell Morphology of the Green Mussel *Perna viridis* (Linnaeus, 1758) (Bivalvia, Mytilidae)

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Abstract: In order to aid identification of larval and post-larval stages of mytilid species, the green mussel *Perna viridis*, we describe morphological features of larval and post-larval shells of *P. viridis* using both an optical microscope and SEM. The features are based on specimens obtained by artificial rearing in laboratory. Umbo and post-larval stages of *P. viridis* are clearly distinguished from the other mytilids that have been described by past studies, except *P. canaliculus* and *P. perna.*

Key Words: larvae, post-larvae, green mussel, *Perna viridis*, shell morphology

In 1998, we started a project to clarify the larval recruitment processes of the green mussel *Perna viridis* (Linnaeus,1758) in Thailand. Success or failure of our project would depend on whether or not we are able to get enough information on morphological features of larval and post-larval shells of the green mussel, by which the larvae in plankton samples and the post-larvae in sediment samples are quickly identified. Identification of larval mytilids is usually based on hinge morphology (Chanley and Andrews, 1971; Le Pennec, 1980; Lutz and Kennish, 1992). Recently, SEM has made it possible to clarify detailed morphological features of hinge. Based on the features of hinge from larval to post-larval mytilids, identification of 20 mytilid species may be made available as shown in Table 1. However, in the case of identifying the larvae and post-larvae in a lot of samples in order to clarify larval recruitment processes, it is necessary to distinguish the specimens quickly using an optical microscope. Unfortunately, except Tan (1975) and Siddall (1980), there is very little information on morphological features of larvae and post-larvae of the green mussel, and as a result larval recruitment processes remain open to be clarified.

The green mussel *Perna viridis* has recently been introduced into and settled in Japanese waters (Kajihara, 1996; Hanyu and Sekiguchi, 2000). Information on morphological features of larval and post-larval shells of the green mussel is also vital for clarifying larval recruitment processes by which the green mussel has established its populations in Japanese waters. In Japan, 96 species of Mytilidae have been reported (Higo *et al.*, 1999). Of these, however, morphological features of larval and post-larval shells of only two species *Musculista senhousia* (Benson, 1842) and *Limnoperna fortunei kikuchii* Habe in Kuroda and Habe, 1981 (= *Xenostrobus securis* (Lamark, 1819)) have been described by Sakai and Sekiguchi (1992) and Kimura and Sekiguchi (1994).

In the present study, we describe morphological features of larval and post-larval shells of the green mussel *Perna viridis*.

METHODOLOGY

Since 1983, the green mussel *Perna viridis*, which was introduced from the Philippines, has been cultured commercially in Okinawa, southern Japan (Murakoshi and Kakazu,1986). In the present study, these mussels were used for artificial spawning in the laboratory. In order to induce artificial spawning in the laboratory, six mature specimens of *P. viridis* were put in a water tank (2,000 ml) which was filled with glassfiber (ADVANTEC TOCEL) - filtered seawater (35‰) and kept alive at room temperature of 28°C. The temperature of the tank was first alternated between 20°C and 30°C for one hour and then the specimens were transferred to a room temperature in order to give a stimulus inducing artificial spawning. The fertilized eggs were kept alive at 28°C in a 1,000 l vessel filled with filtered seawater (35‰). When the water was exchanged once a day, dense droplets of *Pavlova lutheri* Green, 1975 cultures were supplied in the vessel. In the course of keeping alive the fertilized eggs and the larvae to post-larvae, several larvae or post-larvae were sampled from the vessel every day or every three days, fixed with 80% alcohol, and then deposited in a small glass vial, which was placed within a refrigerator at 5°C until they were used for morphological examination. Several specimens of the post-larvae with shell lengths of 2,000 µm or more were obtained from the production area for mussel seed run by a commercial company.

Morphological features of larval to post-larval shells and their hinges were examined using an optical microscope and/or SEM (S-4000, Hitachi Seisakusho Ltd.) according to the method by Sakai and Sekiguchi (1990, 1992). For observation using an optical microscope, we stuck a piece of double-sided sticking vinyl tape on a glass slide, cut a triangular slit in the tape, put the specimen onto the cut slit by using a sucker tube, and placed the specimen in the correct upright position using a needle with a minute fragment of the tape on the tip. For observation using SEM, specimens were rinsed in a buffered 1-2% sodium hypochlorite solution, air-dried, and then examined with SEM after putting on the sample stand and performing vacuum deposition of platinum palladium for 11 minutes.

In the present paper, terminology is defined as follows: larvae are the planktonic ones, including both D-shaped and umbo larvae. D-shaped larvae are the ones before forming an umbo on each shell valve, while umbo larvae are the ones after forming an umbo on the valve until those settle onto the bottom sediment. Post-larvae are the ones shortly after the larvae settle onto the bottom. Post-larvae that have successfully completed settlement and metamorphosis are often referred to as 'Plantigrades' (Bayne, 1976). Terminology for hinge and teeth in larval and post-larval shells follows Fuller and Lutz (1989) as shown in Fig. 1. Shell length is the greatest dimension along any axis of the shell.

RESULT

Growth (Fig. 2)

Our experiments for culturing larvae and post-larvae of the green mussel *Perna viridis* were undertaken at a room temperature of 28°C under ample food conditions. The results are summarized as follows.

It took 24 hours from fertilization to D-shaped larvae which reached an average shell length of 83 (S.D. ± 8) µm. The period for D-shaped larvae was variable, the larvae being found for eight days from one to seven days after fertilization, so that their shell lengths were in the range of 75-140 µm. It took seven days after fertilization to umbo larvae, which reached an average shell length of 161 (S.D. ± 11) µm. The period for umbo larvae was variable, the larvae being found for nine days from seven to 15 days after fertilization, so that their shell lengths were in the range of 140-380 µm. It took 15 days and more from fertilization to larval settlement and/or beginning of post-larval stages. The larvae at settlement reached an average shell length of 357 (S.D. ± 20) µm, their shell lengths being in the range of 300-400 µm. Post-larvae reached an average shell length of 526 (S.D. ± 135) µm 20 days after fertilization, when we stopped continuing experiments of larval to post-larval cultures in the laboratory. Rough estimates of the density of larvae from D-shaped larvae to larval settlement were equivalent to 1 ind. per ml, indicating that the larvae were kept alive under good conditions.

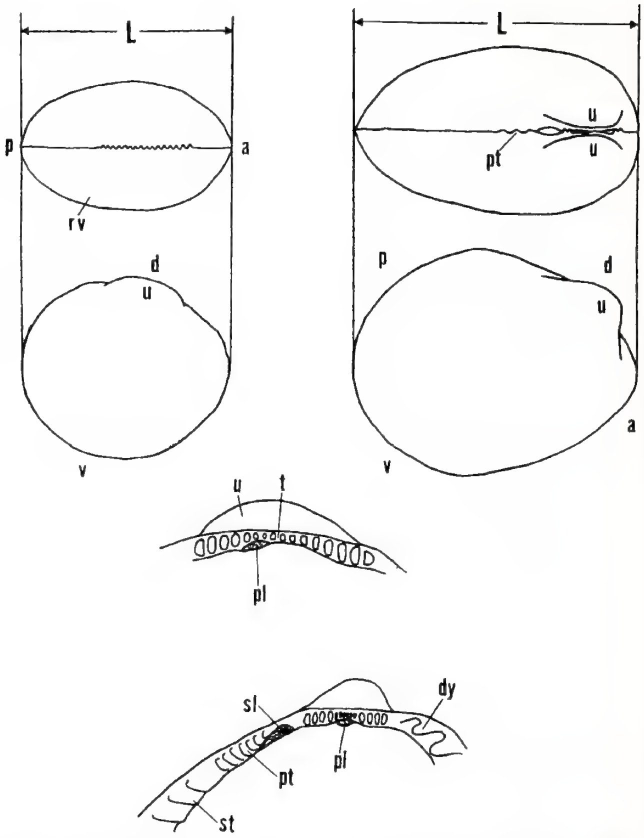

Fig. 1. Terminology for umbo larval and post-larval shells and their hinges in Mytilidae (modified in part from Kimura & Sekiguchi,1994). L: shell length, a: anterior, d: dorsal, dy: dysodont teeth, p: posterior, pl: primary ligament, pt: primary lateral teeth, rv: right valve, sl: secondary ligament, st: secondary lateral teeth, t: teeth, u: umbo, v: ventral.

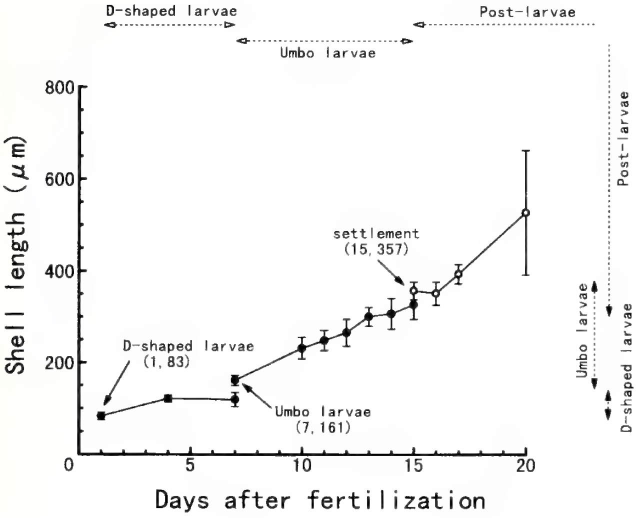

Fig. 2. Growth from D-shaped larvae to post-larvae of the green mussel *Perna viridis* in laboratory. Solid and open circles: data for larvae before and after larval settlement, respectively. Numbers in parentheses: left, days after fertilization; right, average shell length (μm). Dotted lines with open and solid arrows: periods and shell lengths for different stages from D-shaped larvae to post-larvae, respectively.

Observations by optical microscope (Figs. 3 and 4)

Shell shape: D-shaped and umbo larvae have shell lengths of 75-140 μm and 140-380 μm, respectively. Umbo larvae are oval in shape with a round posterior margin and a pointed anterior one, the umbo being located at the middle portion of the shell. In post-larvae (shell length of 300 μm and more but less than 700 μm), shells grow along the postero-ventral margin and the umbo moves toward the anterior margin so that the shell becomes triangular in shape. Also in post-larvae (shell length of 700 μm and more), shells grow along the antero-ventral margin, and gradually slope from the postero-dorsal margin toward the postero-ventral one. Especially for the post-larvae (shell length of 2,000 μm and more), the umbo is located at the anterior margin.

Shell color: D-shaped and umbo larvae lack any color patttern. Post-larvae (shell length of 500 μm and more but less than 2,000 μm) have narrow brown zones around the ventral margin of the shell, while others (shell length of 2,000 μm and more) are with a bright-green zone along the ventral margin.

Hinge: D-shaped larvae (shell length 125 μm) have fine, numerous teeth that are smaller in the middle portion. Umbo larvae (shell length 263 μm) have teeth that are smaller in the middle portion. A post-larva (shell length 338 μm) has a space between the left and right shell valves in the portion from the posterior teeth to the primary lateral teeth. In a post-larva (shell length 451 μm) having fused median teeth, which are difficult to observe due to the growing umbo, the space becomes wider between the posterior teeth and primary lateral teeth. It was difficult to observe the primary and secondary ligament from D-shaped larvae to post-larvae.

Observations by SEM (Figures 5 and 6)

Hinge: D-shaped larvae (shell length ca. 80 μm) show weak dentition as fine, numerous (at least 11 or more) teeth on the left and right shell valves, respectively. Umbo larvae (shell length 144 μm) show 17 and 18 teeth at the left and right shell valves, respectively, while one (shell length of 233 μm) shows 23 and 22 teeth in the left and

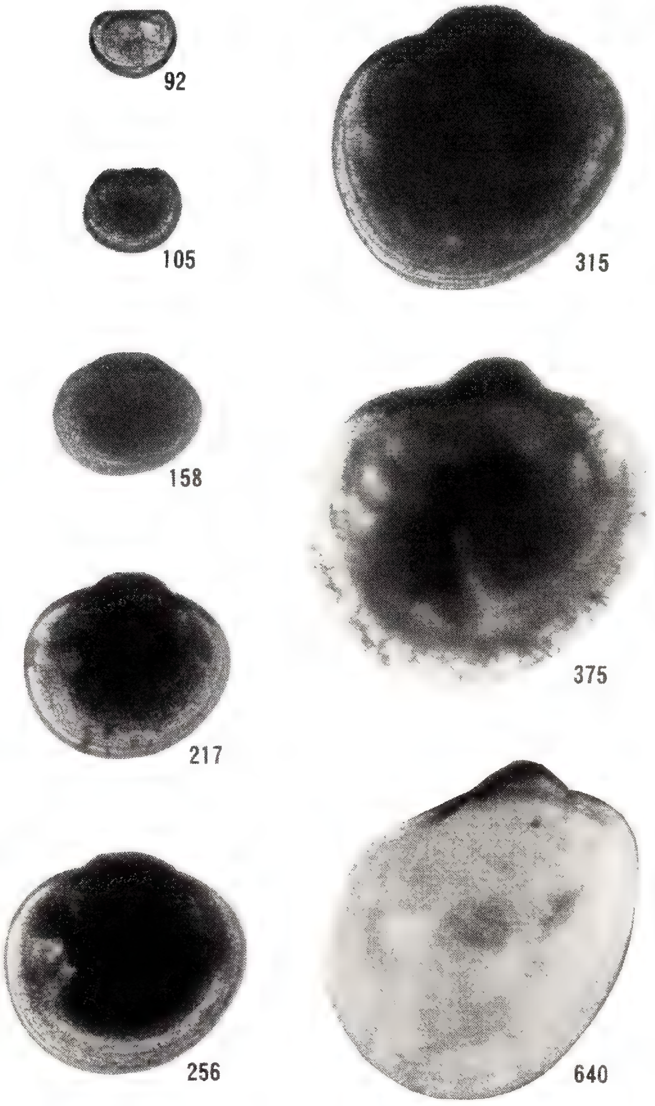

Fig. 3. Optical micrographs of shells of D-shaped, umbo and post-larvae of the green mussel *Perna viridis*. Numbers are shell length (μm). Specimens with shell lengths 315 μm or more belong to post-larvae.

right shell valves, respectively. In a post-larva (shell length 341 µm), the number of the teeth decreases due to the middle teeth fusing with each other, so that post-larvae show 21 and 20 teeth in the left and right shell valves, respectively. Post-larvae (shell lengths 500 µm and more) show the teeth fusing with each other on each shell valve while primary ligaments of those ingrow onto the middle teeth.

Lateral teeth: D-shaped larvae (shell length ca. 80 µm) lack any lateral teeth. Umbo larvae (shell length 240 µm) have primary lateral teeth, their number increasing with growth. Post-larvae (shell length 500 µm and more) have secondary lateral teeth, their number increasing with growth. However, primary lateral teeth degenerate due to development of secondary lateral teeth and also the secondary ligament. Post-larvae (shell length 2,000 µm and more) have 1-3 dysodont teeth, though it was difficult to determine the shell length at which the dysodont teeth appear.

Ligament: D-shaped larvae (shell length ca.80 µm) lack any ligament. Umbo larvae (shell length 240 µm) have a primary ligament, the ligament developing below the middle teeth and encroaching on the teeth with growth. In post-larvae (shell length 400 µm), the secondary ligament develops in front of the primary lateral teeth, while in others (shell length 400 µm and more) the ligament is extended toward the teeth also below the primary lateral teeth.

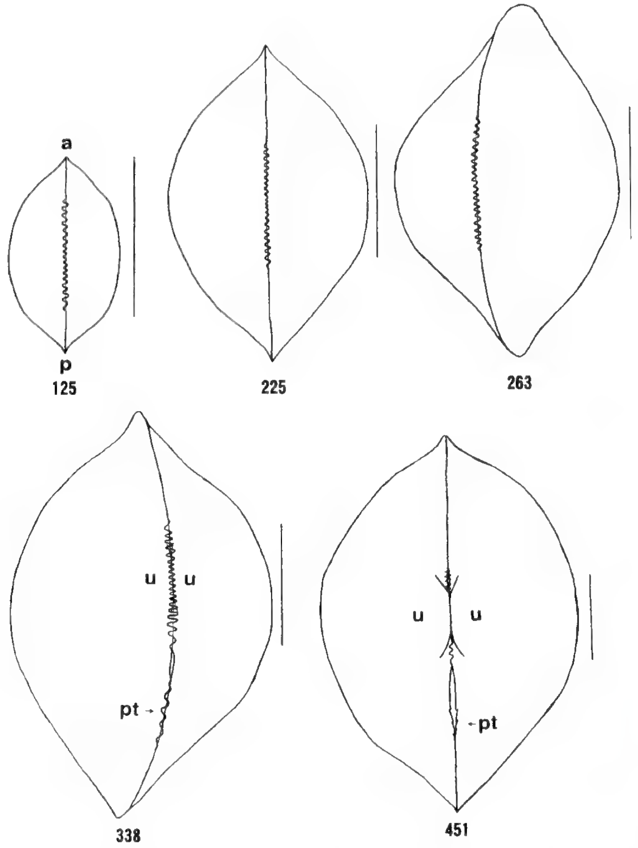

Fig. 4. Drawings from optical micrographs of hinges of D-shaped larvae to post-larvae of the green mussel *Perna viridis*. Numbers are shell length (µm). Scale bars: 100 µm. Symbols are same as in Figure 1. Specimens with shell lengths 338 µm or more belong to post-larvae.

DISCUSSION

Unfortunately, as indicated in Table 1, definitions of post-larvae vary depending on references, so that it is

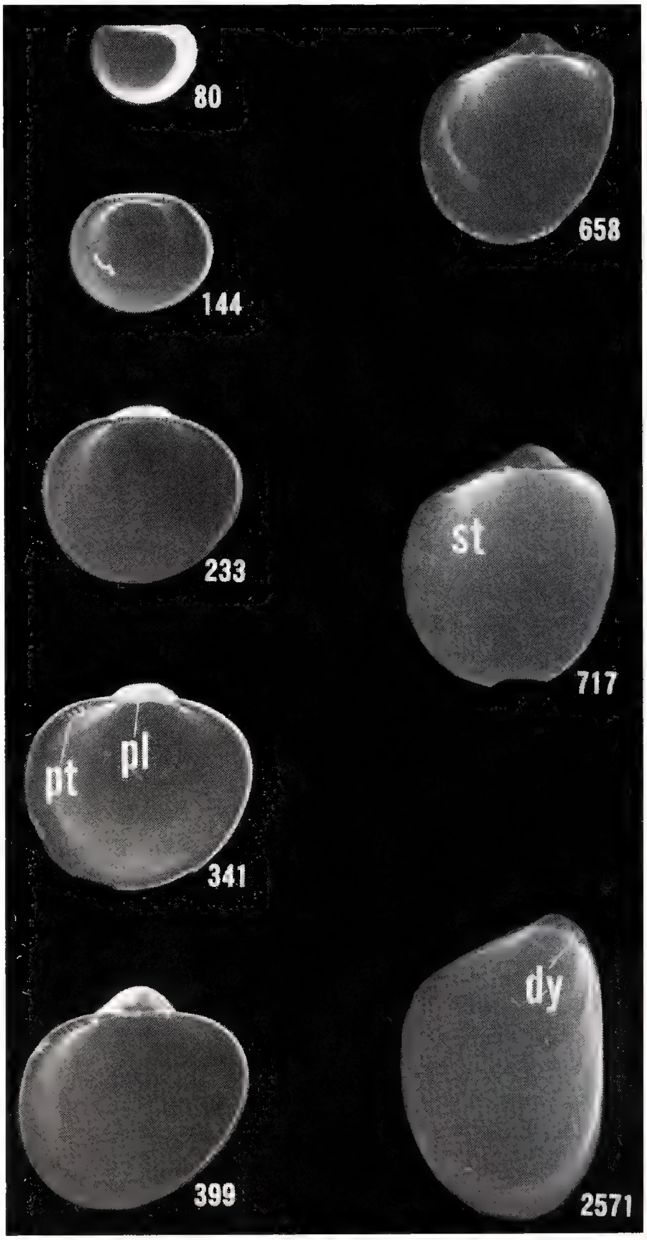

Fig. 5. SEM pictures of shells of D-shaped larvae to post-larvae of the green mussel *Perna viridis*. Numbers are shell length (µm). Symbols are same as in Figure 1.

difficult to compare umbo and post-larvae of different mytilid genera directly. However, umbo larvae of mytilid genera are distinguishable from each other by the presence or absence of the lateral teeth and ligament if the features of post-larvae are different, while D-shaped ones are not distinguishable by the above features.

The genus *Perna* includes three species, *P. canaliculus* (Gmelin, 1791) found in New Zealand waters, *P. perna* (Linnaeus, 1758) in the Red Sea, the east coasts of South Africa, part of the Mediterranean Sea, the east coast of South America south of central Brazil, and part of the Caribbean Sea, and *P. viridis* in the Indo-West Pacific (Siddall, 1980, Vakily, 1989). Taking into account frequent trans-oceanic traffic of commercial ships, these *Perna* species would often have chances to be introduced into the waters where no *Perna* species has yet to be found or where one *Perna* species has already inhabited. If we had such a situation, it would be important to distinguish larvae and post-larvae among the *Perna* species. However, larvae and post-larvae of these three *Perna* species are not distinguishable from each other (see Table 1) and also on the other morphological features described by Siddall (1980), Redfearn *et al.* (1986) and the present study. Other techniques must be applied to identify species, such as using DNA analysis, isozyme analysis, or antigen-antibody reaction.

For clarifying the larval recruitment processes of the green mussel *Perna viridis* in Thailand and Japan, we have to distinguish larvae and post-larvae of the species from the other mytilids, particularly from those of *Arcuatula arcualata* (Hanley, 1843) and *Modiolus* sp. that are common and dominant in Thailand (Dr. K. Chalermwat, pers. comm.) and also from those of the three mytilids (*Mytilus galloprovincialis* Lamarck, 1819, *Xenostrobus securis*, and *Musculista senhousia*) in Japan.

In the following we examine features to distinguish umbo and post-larvae of the genus *Perna* from those of the four mytilid genera (*Mytilus, Musculista, Xenostrobus*, and *Modiolus*) except the genus *Arcuatula,* which lacks detailed information (Le Pennec and Masson, 1976; Lutz and Hidu, 1979; Le Pennec, 1980; Fuller and Lutz, 1989; Sakai and Sekiguchi, 1992; Kimura and Sekiguchi, 1994).

Perna vs. *Mytilus*

Umbo and post-larvae of *Mytilus* lack the primary lateral teeth in contrast to the situation in *Perna*. Post-larvae (shell length of 400 µm or more) of *Mytilus* share shells growing along the posterior margin. For post-larvae (shell length of 2,000 µm or more), the umbo is located more anteriorly in *Perna* than in *Mytilus*.

Perna vs. *Xenostrobus*

Post-larvae of *Xenostrobus* have shells growing much along the posterior margin. The primary ligament in

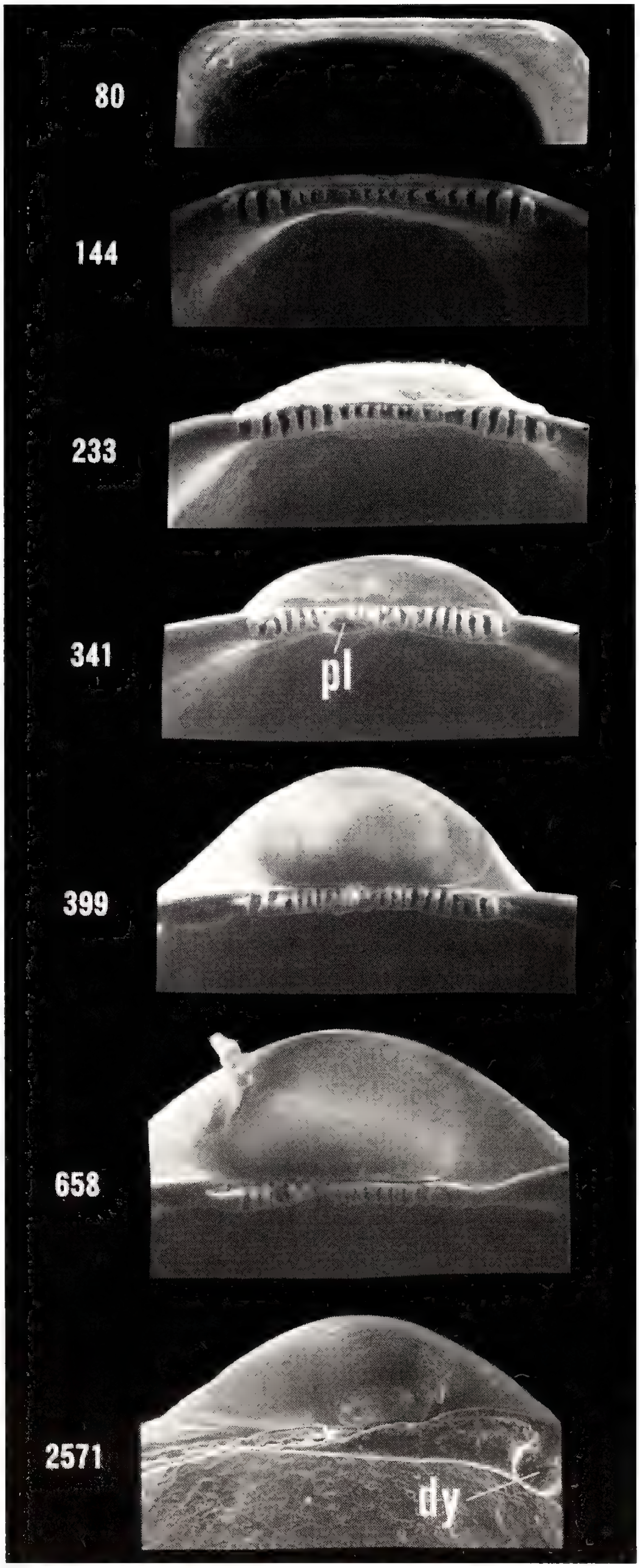

Fig. 6. SEM pictures of hinges of D-shaped, umbo and post-larvae of the green mussel *Perna viridis*. Numbers are shell length (µm). Symbols are same as in Figure 1.

Table 1. Presence of lateral teeth and ligaments in umbo and post-larval mytilids.

Species	Stage	lateral teeth			ligaments		ref.[4]
		pt	st	dy	pl	sl	
Amygdalum papyrium	D-shaped	–	–	–	–	–	1
(Conrad, 1846)	Umbo	–	–	–	–	–	
	Post-larval[1]	–	–	–	+	+	
Aulacomya ater	D-shaped	–	–	–	–	–	2
(Molina, 1782)	D-shaped	–	–	–	–	–	
	Post-larval[1]	–	?	?	+	–	
Brachidontes exustus	D-shaped	–	–	–	–	–	1
(Linnaeus, 1758)	Umbo	–	–	–	–	–	
	Post-larval	+	+	+	+	+	
B. granulata	D-shaped	–	–	–	–	–	2
(Hanley, 1843)	Umbo	–	–	–	–	–	
	Post-larval	+	?	?	+	?	
Choromytilus chorus	D-shaped	–	–	–	–	–	2
(Molina, 1782)	Umbo	–	–	–	–	–	
	Post-larval	–	+	+	+	?	
Geukensia demissa	D-shaped	–	–	–	–	–	1
(Dillwyn, 1817)	Umbo	–	–	–	–	–	
	Post-larval[1]	–	–	–	+	+	
Ischadium recurvum	D-shaped	–	–	–	–	–	1
(Rafinesque, 1820)	Umbo	–	–	–	–	–	
	Post-larval[1]	–	–	+	+	+	
Modiolus modiolus	D-shaped	–	–	–	–	–	1,3
(Linnaeus, 1758)	Umbo	–	–	–	–	–	
	Post-larval[1]	+	–	–	+	+	
Modiolarca impacta	D-shaped	–	–	–	–	–	9
(Herman, 1783)	Umbo	–	–	–	–	–	
	Post-larval	+	?	?	?	?	
Musculista senhousia	D-shaped	–	–	–	–	–	7
(Benson, 1842)	Umbo	–	–	–	+	–	
	Post-larval	+	+	+	+	+	
Mytilus chilensis	D-shaped	–	–	–	–	–	2
Hupe, 1842	Umbo	–	–	–	+	–	
	Post-larval	–	+	+	+	?	
M. edulis	D-shaped	–	–	–	–	–	1,3,4
Linnaeus, 1758	Umbo	–	–	–	–(+)[3]	–	
	Post-larval[1]	–	+	+	+	+	
M. galloprovincialis	D-shaped	–	–	–	–	–	4,5,6
Lamarck, 1819	Umbo	–	–	–	+	–	
	Post-larval	–	+	+	+	+	
Perumytilus purpuratus	D-shaped	–	–	–	–	–	2
(Lamarck, 1819)	Umbo	–	–	–	+	–	
	Post-larval	+	+	?	+	?	
Perna canaliculus	D-shaped	–	–	–	–	–	8,9
(Gmelin, 1791)	Umbo	+	–	–	+	–	
	Post-larval[2]	+	+	+	+	+	
P. perna	D-shaped	–	–	–	–	–	8
(Linnaeus, 1758)	Umbo	+	–	–	+	–	
	Post-larval[2]	+	+	+	+	+	
P. viridis	D-shaped	–	–	–	–	–	8,10
(Linnaeus, 1758)	Umbo	+	–	–	+	–	
	Post-larval	+	+	+	+	+	
Semimytilus algosus	D-shaped	–	–	–	–	–	2
Gold, 1850	Umbo	–	–	–	–	–	
	Post-larval	+	+	?	+	?	
Xenostrobus pulex	D-shaped	–	–	–	–	–	9
(Lamarck, 1819)	Umbo	–	–	–	+	–	
	Post-larval	–	?	?	?	?	
X. securis	D-shaped	–	–	–	–	–	7
(Lamarck, 1819)	Umbo	–	–	–	+	–	
	Post-larval	–	–	–	+	+	

[1] Definitions are problematic, because beginning of the Post-larval stage, *i.e.* after metamorphosis, is defined as occurrence of primary ligament in Fuller & Lutz (1989) and Le Pennec (1980).

[2] Defined as Plantigrades in Siddall (1980).

[3] Data for *Mytilus edulis aoteanus* in New Zealand waters (Redfearn *et al.*, 1986).

[4] 1. Fuller and Lutz (1989), 2. Ramorino and Campos (1983), 3. Lutz and Hidu (1979), 4. Le Pennec (1980), 5. Sakai and Sekiguchi (1992), 6. Le Pennec and Masson (1976), 7. Kimura and Sekiguchi (1994), 8. Siddall (1980), 9. Redfearn *et al.* (1986), 10. the present study

Xenostrobus is found below the posterior teeth. Umbo larvae of *Xenostrobus* do not have teeth that are smaller in the middle. Post-larvae of *Xenostrobus* do not have lateral teeth, in contrast to the siutation in *Perna*.

Perna vs. *Musculista*

Post-larvae (shell length of 400 µm or more) of *Musculista* have shells growing along the posterior margin. *Musculista* has the primary ligament clearly visible through the hinge from the dorsal view. The secondary ligament develops in *Musculista* for those with shell lengths of 550 µm or more. Primary lateral teeth develop in *Musculista* with shell length of 500 µm and more. *Musculista* does not have a wider space between primary lateral teeth and posterior teeth of the two shell valves. For shell lengths of 700 µm or more the umbo is located more anteriorly in *Perna* than in *Musculista*.

Perna vs. *Modiolus*

Only primary lateral teeth are found in shell lengths of 542 µm or more in *Modiolus*. *Modiolus* has a relatively larger primary ligament than does *P. viridis*. For shell lengths of 700 µm or more, the umbo is located more anteriorly in *Perna* than in *Modiolus*.

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Latitudinal trends in naticid predation on *Anadara ovalis* (Bruguière, 1789) and *Divalinga quadrisulcata* (Orbigny, 1842) from New Jersey to the Florida Keys

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Abstract: Predation indices commonly calculated to quantify the interaction between drilling naticid gastropods and their bivalve prey include borehole-site stereotypy, predator-prey size selectivity, prey- size class preference, size refuge from predation, prey effectiveness (PE) and predation intensity (PI; synonymous with drilling frequency or incidence of drilling in the literature). The indices were calculated for samples of the blood ark *Anadara ovalis* (Bruguière, 1789) (six sites; n = 2023, collectively) and the cross-hatched lucine *Divalinga quadrisulcata* (Orbigny, 1842) (five sites; n = 2597, collectively) from New Jersey (Virginian molluscan subprovince) to the Florida Keys (Caribbean molluscan province). Borehole sites are concentrated on the ventral margin in New Jersey and the dorsal margin in South Carolina and Florida on valves of *D. quadrisulcata*, with a North Carolina site showing a bimodal distribution for the umbos and the ventral margin. This latitiudinal shift in borehole-site stereotypy is attributed to a different suite of naticid species drilling *D. quadrisulcata* in the northern vs. southern populations. *Euspira heros*, (Say, 1822) and *Neverita duplicata* (Say, 1822) drill the cross-hatched lucine north of the Chesapeake Bay, whereas *Sinum perspectivum* (Say, 1831), *Polinices lacteus* (Guilding, 1834), and *Naticarius canrena* (Linnaeus, 1758) and other naticid species drill populations of the cross-hatched lucine in the Outerbanks and further south. No such latitudinal shift in stereotypy is evident for *A. ovalis;* complete boreholes are invariably concentrated on the exposed umbos of the hairy periostracum-veneered, semi-infaunal blood ark at all sampled latitudes. No size refuge from predation is evident for *D. quadrisulcata* at any latitude as the largest size classes are bored at each sample site. In contrast, *A. ovalis* has a size refuge at each locality, with the largest unbored specimens at least 10 mm greater than the largest bored specimen. Nevertheless, maximum size of a bored valve does not increase or decrease across the latitudes. Prey size selectivity by naticids shows no pattern from New Jersey to Florida for either bivalve species. Correlations between predator size, indexed by the outer borehole diameter (OBD) in the valve, and prey size (length or width) are significant for only three of 11 samples combined for both species. Prey effectiveness increases for *D. quadrisulcata* from north to south, suggesting that this bivalve prey more frequently escaped from foot-envelopment by the smaller southern naticids (< mean OBD). In contrast, incomplete boreholes are very infrequent on *A. ovalis*, which is a sluggish, semi-infaunal burrower that cannot elude the enveloping naticid foot. Although possibly complicated by taphonomic biases, as is PE, predation intensity increases for both species from the Virginian Subprovince to the Caribbean Province. In northern latitudes, the copious, large surfclam *Spisula solidissima* (Dillwyn, 1822) is the preferred naticid prey. But south of the Chesapeake, naticids increasingly drill *D. quadrisulcata* and *A. ovalis* as part of the alternative bivalve prey to the vanishing surfclams.

Key Words: naticids, predation, stereotypy, *Divalinga quadrisulcata, Anadara ovalis*

Quantification of modern predatory naticid-bivalve prey interaction has been generated to a large extent from beach assemblages of disarticulated bored and unbored valves (Franz, 1977; Vignali and Galleni, 1986; Dietl and Alexander, 1997). Naticid borehole-site stereotypy (Carriker, 1981; Kabat, 1990a), on bivalve shells may be concentrated dorsally near the valve beak (Dietl and Alexander, 1997; Vignali and Galleni, 1986; Ansell and Morten, 1985; Kitchell *et al.*, 1981), whereas others clams have drillholes mostly near the ventral shell margin (Ansell, 1960; Griffiths, 1981; Bayless, 1986; Vermeij *et al.*, 1989). Region of concentration of borehole sites on the valve may vary among congeneric bivalve prey species (Anderson, 1992). Prey size-selectivity has also been documented for naticid predation (Kitchell *et al.*, 1981; Kelley, 1988; Dietl and Alexander, 1997). Bivalve prey effectiveness (PE) in deterrence of naticid drilling is indexed by the ratio of incomplete boreholes to total attempts (Vermeij *et al.* 1989), a calculation that has been applied to several species (Vermeij, 1987). Another useful index, predation intensity (PI), compares the ratio of bored to total valves in the sample (Vermeij, 1980; Vermeij *et al.*, 1989). The index is synonymous with drilling frequency and incidence of drilling in the published literature. Temporal patterns in stereotypy of drillhole site, prey size selectivity, and PE have been reconstructed (Kelley and Hansen, 1993, 1996a, 1996b) to test hypotheses of escalation through time (Vermeij, 1987).

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Despite establishment of temporal patterns (Kelley and Hansen, 1993, 1996a, 1996b), published investigations of naticid-bivalve interactions that focus on latitudinal gradients or patterns in stereotypy, prey size selectivity, PE, and PI that involve geographically wide ranging bivalve species are notably wanting. Vermeij *et al.* (1989) concluded from a variety of bivalve species at different latitudes that the average cool temperature species had a higher incidence of drilling (24%) than tropical species (9%). However, Vermeij (1993) subsequently doubted the feasibility that latitudinal trends could be documented. He stated that "given the great variation in the importance of drilling from place to place as well as among species at single sites, a latitudinal pattern would be difficult to prove even if more extensive surveys were in hand."

This deficiency in documentation of latitudinal trends belies the geographic variations in naticid species richness and modal size, moonsnail density and mobility, and morphologic and habit variation in the bivalve prey. Combined, these variables could significantly alter the above mentioned predation indices from temperate to subtropical latitudes. Naticid species richness on the U.S. Atlantic Coast increases from Maine to the Florida Keys (Abbott, 1968; Abbott and Dance, 1983; Kabat, 1990b), a situation paralleled on the eastern side of the Atlantic (Taylor and Taylor, 1977). As naticid species in southern latitudes replace those from northern latitudes, increases or decreases in size of predatory moonsnails could result in shifts in borehole site stereotypy on the valves of conspecific bivalve prey populations. Even if the dominant predatory naticid species is the same across many degrees of latitude, intraspecific changes in modal size of the predator and/or prey could influence correlations between predator and prey size, as well as PE. Dietl and Alexander (1997) noted dramatically different PE values for the surfclam *Spisula solidissima* (Dillwyn, 1817) from Long Island to Delaware, a range dominated by the naticid *Euspira heros* (Say, 1822) to the north, and *Neverita duplicata* (Say, 1822) to the south, of Atlantic City, New Jersey. Moonsnail locomotion rates on the surface vary considerably among naticids (Lindsey, 1978) which in turn could affect foraging success at the sediment surface for semi-infaunal bivalve prey. Burrowing rate indices vary by a factor of seven (0.19 to 1.38) among naticids (Trueman and Brown, 1992), which could influence the success rate in capture of infaunal clams. Furthermore, clam burrowing rate, which could influence bivalve escape potential from burrowing naticids, varies with sedimentological texture (Alexander *et al.*, 1993) and temperature regimes (Ansell, 1985). Both nearshore, sedimentological texture regimes (Edwards, 1988) and mean annual water temperature in coastal waters vary from Massachusetts to the Florida Keys.

Ideal candidates for investigation of possible differences in stereotypy, prey size selectivity, PE, and PI along the Atlantic Coast of the United States are the blood ark *Anadara ovalis* (Bruguière, 1789) and the cross-hatched lucine, *Divalinga quadrisulcata* (Orbigny, 1842) (Fig. 1). These species range from Massachusetts to the Gulf Coast and from Massachusetts to Brazil, respectively, an expanse that includes the Carolinian Province (Atlantic and Gulf Component), the Palm Beach Provinciatone, the Caribbean Province and the Brazilian Province (Petuch, 1988). Abbott (1968) delimited the Virginian Subprovince within the Carolinian Province of the Atlantic Coast, a delineation we adopt in this investigation based on differences in molluscan composition in communities above and below Cape Hatteras, North Carolina, where the southward flowing Labrador Current and the northward flowing Gulf Stream converge (Coomans, 1962).

Divalinga quadrisulcata is a relatively small (maximum shell width = 30 mm on U. S. Atlantic Coast and in Brazil [Couto, 1996]), compressed, ovate clam, with fine, chevron-shaped concentric ornamentation (Fig. 1) that facilitates burrowing (Stanley, 1970). The species is a moderately slow burrower that penetrates sediment to depths of 10-20 cm beneath the surface in clean, moderately well sorted, fine to very fine grained sand (Stanley, 1970). Once burrowed to its depth limit, the clam rotates its valves so that the plane between them is parallel to the sediment surface. The species lives from intertidal sandflats (Stanley, 1970) to water depths of 70 m (Abbott, 1968). *Anadara ovalis* is a very slow burrower (Stanley, 1970; Alexander, 1993) and is epibyssate as a juvenile. In adulthood, the inflated, radially ribbed clam lives unattached and mostly buried with its umbonal region protruding above the sediment surface (Alexander, 1993). The hairy periostracum typically veneering the radially ribbed valves is often abraded from the beaks of live semi-infaunal individuals. Inhabited substrata are highly variable, including sands, muddy sands (Stanley, 1970), and gravelly, muddy sands (Alexander, 1993). The species dwells in water depths ranging from 1 to 30 m (Abbott, 1968).

Shallow water moonsnail predators on both of these clams vary among molluscan (sub)provinces (Fig. 1). In the Virginian Subprovince, *Euspira heros* (fomerly *Lunatia heros*) and *Neverita duplicata* (fomerly *Polinices duplicatus*) are the largest of all naticids on the Atlantic Coast (Fig. 1), with *N. duplicata* replacing *E. heros* in abundance in nearshore habitats south of Barnegat Inlet, New Jersey (Dietl and Alexander, 1997). Also found in northern latitudes is the uncommon *E. triseriata* (Say, 1822). Along the Outerbanks, North Carolina, where the Virginian Subprovince terminates, *Sinum perspectivum* (Say, 1831) (Fig. 1) is locally more abundant than *N. duplicata* in nearshore sandy habitats as evidenced by sampling by the authors. *P. lacteus* (Goulding, 1834) (Fig. 1) is another

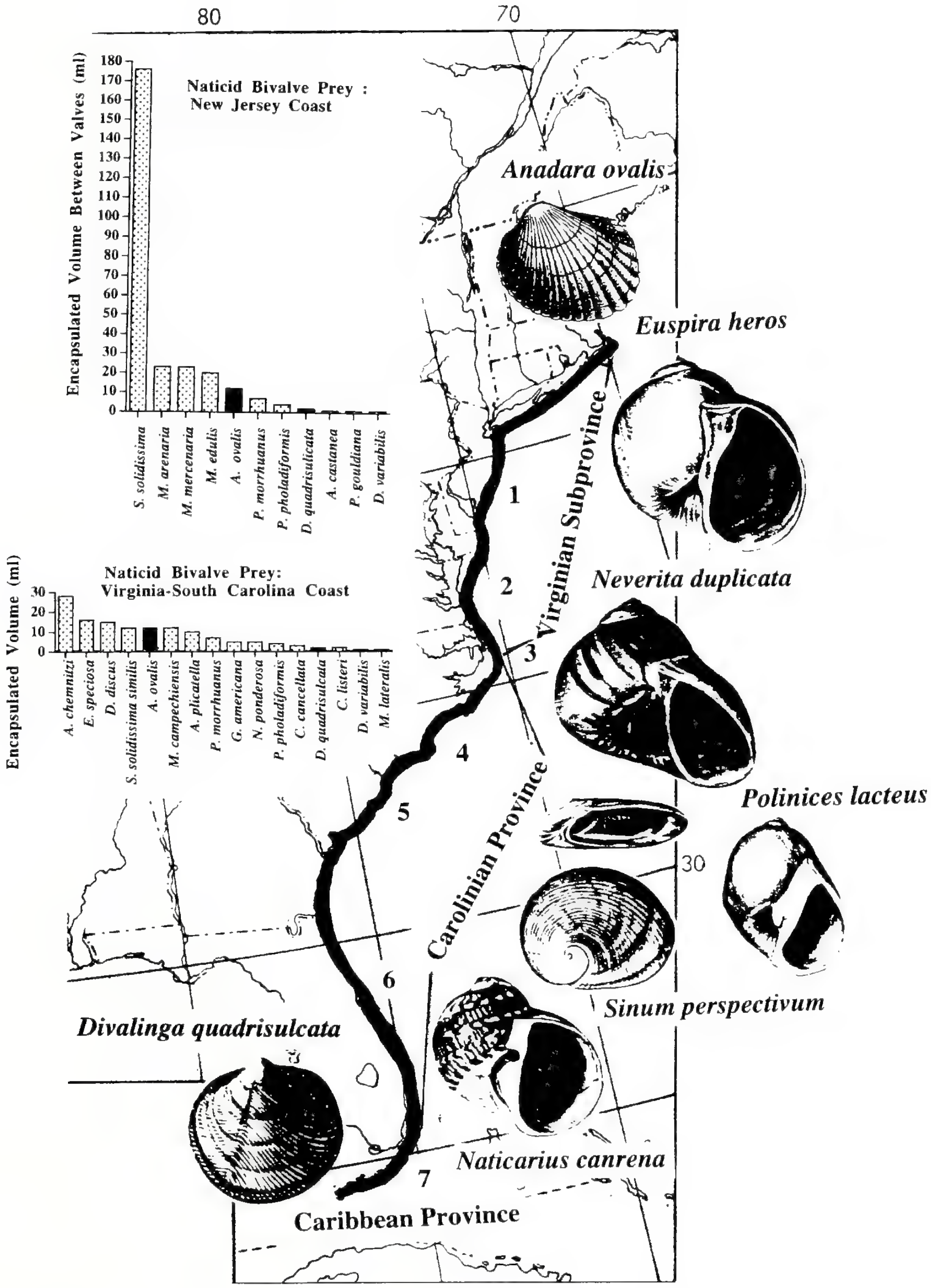

80
70
Naticid Bivalve Prey : New Jersey Coast
Encapsulated Volume Between Valves (ml)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
S. solidissima
M. arenaria
M. mercenaria
M. edulis
A. ovalis
P. morrhuanus
P. pholadiformis
D. quadrisulcata
A. castanea
P. gouldiana
D. variabilis
Naticid Bivalve Prey: Virginia-South Carolina Coast
Encapsulated Volume (ml)
0
10
20
30
A. chemnitzi
E. speciosa
D. discus
S. solidissima similis
A. ovalis
M. campechiensis
A. plicatella
P. morrhuanus
G. americana
N. ponderosa
P. pholadiformis
C. cancellata
D. quadrisulcata
C. listeri
D. variabilis
M. lateralis
Anadara ovalis
Euspira heros
Virginian Subprovince
Neverita duplicata
Carolinian Province
Polinices lacteus
30
Sinum perspectivum
Divalinga quadrisulcata
Naticarius canrena
Caribbean Province
1
2
3
4
5
6
7

Fig. 1. Sampling localities and latitudinal range of the bivalves *Divalinga quadrisulcata* and *Anadara ovalis* among molluscan (sub) provinces of the eastern coast of the U. S. A. Illustrated naticids (not to scale) are common to various sampling localities. 1, Hereford Inlet, Stone Harbor, New Jersey *(Neverita duplicata)*, 2, First Landing State Park, Norfolk, Virginia (*A. ovalis* only), 3, Kill Devil Hills Beach, North Carolina *(Sinum perspectivum)*, 4, Wrightsville Beach, North Carolina, 5, Litchfield Beach, South Carolina, 6, Cocoa Beach, Melbourne, Florida (*A. ovalis* only), 7, Bahia Honda Key, Florida (*D. quadrisulcata* only). Encapsulated volume of bivalves (ml) determined by twice the volume of sand held by a single valve with the same DV length as the largest bored valve of that species in the molluscan (sub)province. *S. solidissima = Spisula solidissima; M. arenaria =Mya arenaria; M. mercenaria = Mercenaria mercenaria; M. edulis = Mytilus edulis; A. ovalis = Anadara ovalis; P. morrhuanus = Pitar morrhuanus; P. pholadiformis = Petricola pholadiformis; D. quadrisulcata = Divalinga quadrisulcata; A. castanea = Astarte castanea; P. gouldiana = Pandora gouldiana; D. variabilis = Donax variabilis; A. chemnitzi = Anadara chemnitzi; E. speciosa = Eucrassatella speciosa; D. discus = Dosinia discus; M. campecheiensis = Mercenaria campechiensis; A. plicatella = Anatina plicatella; G. americana = Glycymeris americana; N. ponderosa = Noetia ponderosa; C. cancellata = Chione cancellata; C. listeri = Chione listeri; M. lateralis = Mulinia lateralis.*

small naticid that is common in nearshore sands from the Carolinas to the Florida Keys (Abbott and Dance, 1983). Naticids in nearshore habitats from North Carolina to Florida also include the uncommon (Abbott and Dance, 1983) *Tectonatica pusilla* (Say, 1822) and *Sinum maculatum* (Say, 1831). In the Florida Keys of the Caribbean Province, *Naticarius canrena* (Linnaeus, 1758) (Fig. 1) is very common (Abbott and Dance, 1983) in very shallow subtidal carbonate sand flats with turtle grass (Alexander, personal observations). Smaller in size, but also moderately common in the Florida Keys (Abbott and Dance, 1983) is *Natica marochiensis* (Gmelin, 1791). Much less common in the Florida Keys is *Polinices hepaticus* (Röding, 1798) (Abbott and Dance, 1983), although this species is the primary predator on *Divalinga quadrisulcata* on the southeastern coast of Brazil (Couto, 1996). The small *Stigmaulax sulcata* (Born, 1778) and *Natica floridana* (Rehder, 1943) are also uncommon in the Florida Keys (Abbott and Dance, 1983). As a refutable hypothesis, we predict that the different suite of nearshore sandy bottom dwelling naticid species in each of the molluscan (sub)provinces from New Jersey to the Florida Keys, combined with any significant changes in prey mean size and thickness latitudinally, should differentiate borehole-site stereotypy, prey size-selectivity, prey effectiveness, and predation intensity from northern to southern populations of *Anadara ovalis* and *D. quadrisulcata.*

METHODS AND MATERIALS

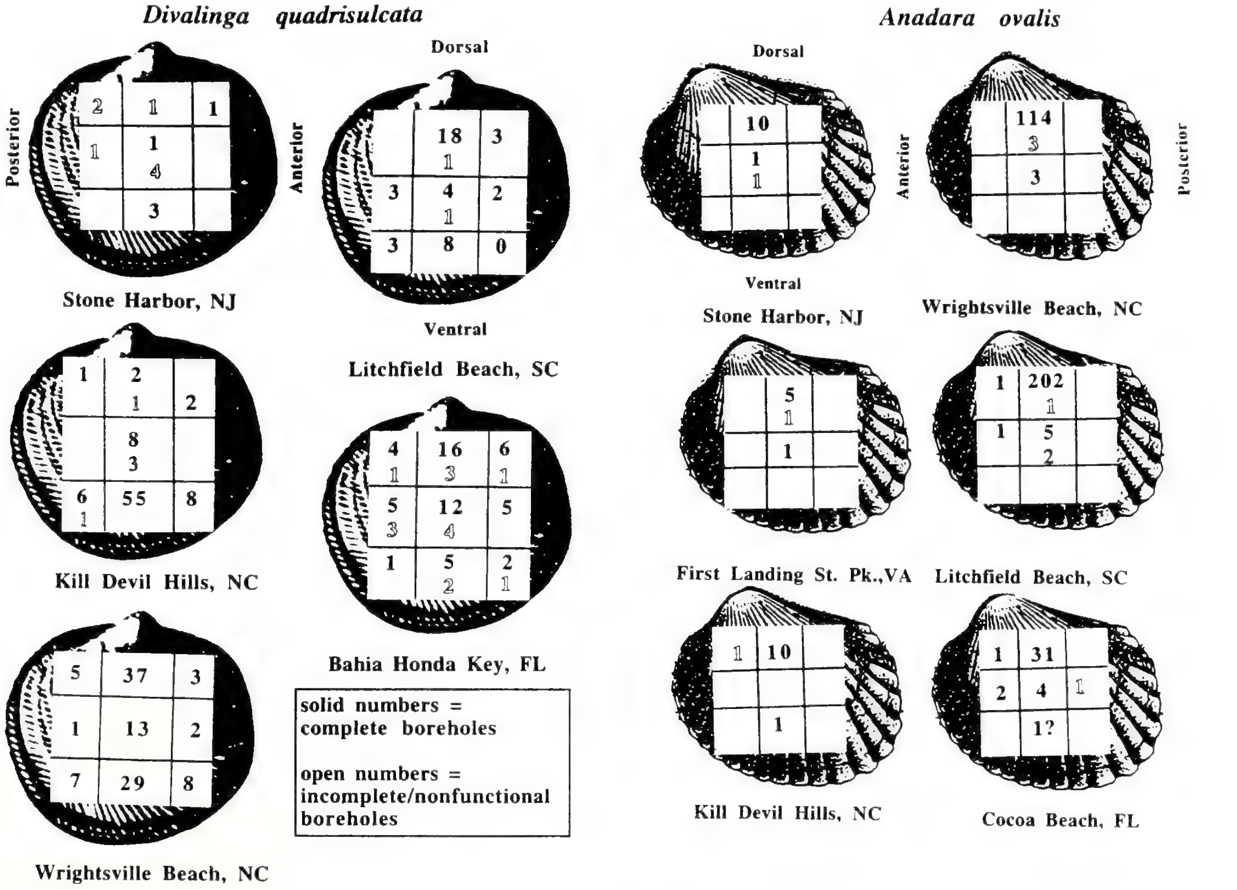
Samples of *Anadara ovalis* and *Divalinga quadrisulcata* were collected from each of the molluscan (sub)provinces (Fig. 1). In the Virginian Subprovince, samples were taken at (1) the Stone Harbor spit near the entrance to Hereford Inlet, Stone Harbor, New Jersey (n = 363 for *A. ovalis*; n = 263 for *D. quadrisulcata*), and (2) Virginia Beach First Landing State Park, Norfolk, Virginia (n = 77 for *A. ovalis*). (3) Near the transition between the Virginian Subprovince and the Carolinian Province in the Outerbanks, North Carolina, samples were collected from the beaches near Kill Devil Hills, North Carolina (*A. ovalis* = 193; *D. quadrisulcata* = 964). Further south in the Carolinian Province, samples were collected from (4) Shell Island at the north end of Wrightsville Beach, North Carolina (n = 125 for *A. ovalis*; n = 609 for *D. quadrisulcata*), (5) Litchfield Beach, South Carolina (n = 221 for *A. ovalis*; n = 237 for *D. quadrisulcata*), and (6) Cocoa Beach, Melbourne, Florida (n = 46 for *A.ovalis*). In the Caribbean province, a sample was collected at (7) Bahia Honda Key, Florida (n = 524 for *D. quadrisulcata*). The initial samples of *A. ovalis* at Wrightsville Beach, North Carolina and Litchfield Beach, South Carolina consisted of bored specimens exclusively and therefore were nonrandom. Subsequently, these two localities were re-sampled in order to obtain a random sample of both bored and unbored shells of the blood ark. Resampling yielded 405 and 593 specimens at Wrightsville Beach and Huntington Beach State Park (adjacent to Litchfield Beach), respectively. All entire-margined invariably disarticulated, shells were collected on the sandy beaches between the high and low tide line along approximately a 1000m strip. The area was resampled on subsequent days until the above mentioned sample sizes were obtained. Broken specimens were excluded because it could not be ascertained if the missing piece, often an umbo, had or did not have a complete or incomplete borehole. Samples are referred to as the NJ (New Jersey), VA (Virginia), NC-K (Kill Devil Hills, North Carolina), NC-W (Wrightsville Beach, North Carolina), SC (South Carolina) and FL-C (Central Florida) and FL-K (Florida Keys) samples hereafter.

Anterior-posterior width of *Divalinga quadrisulcata* and dorsal-ventral length of *Anadara ovalis* on all specimens was measured to the nearest 0.1 mm and size-frequency distributions were plotted. Cumulative-percent frequency distributions of bored (complete and incomplete drillholes) vs. unbored shells were statistically compared by a Kolmogorov-Smirnov test to determine preferred size classes of naticid prey (Dietl and Alexander, 1997). Furthermore, outer borehole diameter (OBD) of both complete and incomplete boreholes (only inner borehole diameter changes during drilling; Kitchell *et al.*, 1986) in the prey shell is a reliable index of predator size as experimentally documented by Kitchell *et al.* (1981). Size (whorl diameter) of the predatory moon snail is closely correlated with clam prey length (Kitchell *et al.*, 1981; Kelley, 1991; Dietl and Alexander, 1997). Accordingly, OBD of complete and incomplete drillholes in the valve of *A. ovalis* and *D. quadrisulcata* was regressed on valve length and width, respectively, for each sample. Mean OBDs in the valves of each species at each locality were compared by one way ANOVA. Fisher PSLD tests distinguished significant differences between compared means when the null hypothesis of equality in the ANOVA test was rejected. Mean dorsal-ventral length of unbored *A. ovalis* and anterior-posterior width of *D. quadrisulcata* were compared (one-way ANOVA) for each species at each locality to determine if the potential prey size is increasing, decreasing, or remaining static from north to south. The procedure was repeated for the bored specimens of each species to determine if preferred size of drilled prey is changing latitudinally. Again, Fisher PSLD tests distinguished significant differences between compared means when the null hypothesis of equality in the ANOVA test was rejected.

Each completely or incompletely bored valve was divided into nine sectors, namely three dorsal, three central, and three ventral divisions. Frequency of complete and incomplete boreholes was calculated for each sector, a procedure utilized by Anderson (1992) and Kelley (1988). A Chi Square Goodness of fit test was performed on each sample to determine borehole site selectivity (disproportional frequencies) among valve regions by naticids drilling *Anadara ovalis* and *Divalinga quadrisulcata* for each locality according to a similar statistical application by Dietl and Alexander (1997). Prey effectiveness in deterring predation, PE, is calculated as the ratio of incomplete boreholes and nonfunctional boreholes (nonfunctional boreholes = outerborehole/inner borehole diameter ratio > 0.5; Kitchell *et al.*, 1986) over the sum of incomplete, nonfunctional, and complete boreholes (= all predatory attempts, successful and unsuccessful) (Vermeij *et al.*, 1989). The ratio is an index of the probability that the prey survived predatory attempts by the moonsnails. Predation intensity, PI, will be calculated by the ratio of twice the number of bored valves (because every disarticulated bored valve once had an adjoining unbored valve) divided by the total number of valves (Vermeij, 1980, Vermeij *et al.*, 1989). Specimens with eroded, missing beaks, which are a common site of boreholes, were excluded from the sample owing to the inability to assign such specimens to either the bored or unbored subset of the sample, a procedure that may either underestimate or overestimate PI. The ratio is an index of the probability that a clam will be killed by a moonsnail in its lifetime. The calculation was precluded on the FL-C sample of *A. ovalis*, for which only bored shells were collected.

RESULTS

Differences in borehole-site stereotypy exist among the five populations of *Divalinga quadrisulcata* (Table 1, Fig. 2), but not *Anadara ovalis* (Table 2, Fig. 2). Concentration of boreholes shifts from the ventral margin in populations from the Virginian Subprovince (NJ and NC-K) to the beak area in populations from the Carolinian and Caribbean Province (SC and FL-K samples) (Fig. 2) for *D. quadrisulcata*. The NC-W sample is transitional between samples to the north and the south; boreholes are bimodally distributed at the beak and ventral margin (Fig. 2). In contrast, boreholes are invariably concentrated at the



Divalinga quadrisulcata
Dorsal
Posterior
Anterior
2 1 1
1 1 4
3
Stone Harbor, NJ
18 3 1
3 4 2 1
3 8 0
Ventral
Litchfield Beach, SC
1 2 1 2
8 3
6 1 55 8
Kill Devil Hills, NC
4 16 6 1 3 1
5 12 5 3 4
1 5 2 2 1
Bahia Honda Key, FL
5 37 3
1 13 2
7 29 8
Wrightsville Beach, NC
solid numbers = complete boreholes
open numbers = incomplete/nonfunctional boreholes
Anadara ovalis
Dorsal
Anterior
Posterior
10
1 1
Ventral
Stone Harbor, NJ
114 3
3
Wrightsville Beach, NC
5 1
1
First Landing St. Pk.,VA
1 202 1
1 5 2
Litchfield Beach, SC
1 10
1
Kill Devil Hills, NC
1 31
2 4 1
1?
Cocoa Beach, FL

Fig. 2. Frequency distribution of complete (solid) and incomplete -nonfunctional (open) boreholes in nine sectors of valves of *Divalinga quadrisulcata* and *Anadara ovalis* for each sampling locality. Specimens not to scale. Methodology after Kelley (1988).

Table 1. Characteristics of naticid predator-*Divaricella quadrisulcata* prey interaction at each locality

Index of Predation	Stone Harbor (SH), NJ	Kill Devil Hills (KDH), NC	Wrightsville Beach (WB), NC	Litchfield Beach (LB), SC	Bahia Honda Key (BHK), FL
Borehole Site Selectivity (Goodness of fit test of sectorized data)	Statistically Indeterminate (but none drilled in beak area)	Preference for ventral margin (Chi square = 250.71; p < 0.001)	Preference for beak & ventral margin (Chi square= 118.79; p < 0.001)	Preference for beak (Chi square = 6.46; p < 0.05)	Preference for beak (Chi square = 31.54; p < 0.001)
Prey size-class preference (& size refuge) (Kolmogorov-Smirnov test)	Indeterminate (Too few bored)	Dmax = 0.099 p = 0.3793 (accept Ho; bored =unbored distribution)	Dmax = 0.138 P = 0.2045 (accept Ho; bored =unbored distribution)	D max = 0.114 p = 0.4961 (accept Ho; bored =unbored distribution)	D max = 0.155 p = 0.222 accept Ho; bored = unbored distribution)
Mean AP width of drilled valves	16.3 mm* n = 13 > KDH, > BHK	13.3 mm* n = 85 < SH, < WB, < LB	14.9 mm* n = 105 > KDH, > BHK	15.1 mm* n = 41 > KDH, > BHK	13.8 mm* n = 64 < SH, < WB, < LB
Mean OBD of complete & incomplete boreholes	1.5 mm* n = 13 < KDH, < WB, < LB	2.2 mm* n = 87 > SH, < WB, < LB, > BHK	2.6 mm n = 105 > SH, > KDH, > BHK	*2.8 mm* n = 41 > SH, > KDH, > BHK	1.4 mm* n = 71 < KDH, < WB, < LB
Mean AP width of unbored valves	16.1 mm n = 270 > all other samples	13.6 mm* n = 877 < all other samples	15.4 mm* n = 495 < SH, > KDH > BHK	15.5 mm* n = 200 < SH, > KDH, > BHK	14.3 mm* n = 460 < SH, > KDH < WB, < LB
Predator-prey size correlation (r value for OBD regressed on valve width)	r = 0.114 p > 0.90 (n = 13)	r = 0.127 p > 0.25 (n = 87)	r = 0.334** p < 0.001 (n = 105)	r = 0.104 p > 0.39 (n = 43)	r = 0.027 p > 0.83 (n = 71)
Prey Efficiency (PE= no. of valves with incomplete & nonfunctional boreholes / total number attempts)	PE = 0.62 8/13	PE = 0.08 7/87	PE = 0.00 0/105	PE = 0.05 2/43	PE = 0.20 14/71
Predation Intensity (PI= number of valves bored X 2 / number of unbored valves)	PI = 0.04 5(x2)/283	PI = 0.17 80(x2)/964	PI = 0.34 102(x2)/600	PI = 0.35 41(x2)/243	PI = 0.21 57(x2)/531

*ANOVA indicates significant difference (p<0.01) among sample means. Significant comparisons of mean by Fisher PLSD indicated by < or >.
** Statistically significant correlation coefficient, r.

beak of *A. ovalis* in each sample regardless of latitude (Fig. 2). In fact, boreholes not situated at the beak constitute only 5% of all blood ark specimens combined for all latitudes.

A major distinction between the two bivalve prey is that naticids did not prefer particular prey size classes among *Divalinga quadrisulcata* (Table 1, Fig. 3), but were prey-size selective on *Anadara ovalis* (Table 2; Fig. 4). Moonsnails bored all size classes of the cross-hatched lucine proportionately based on the Kolmogorov-Smirnov test (Table 1). A size refuge from predation does not exist for this clam species, considering that the largest bored specimens are within a mm of the maximum size of unbored valves for the NC-K, NC-W, SC, and FL samples (Fig. 3). The NJ sample appears to be an exception, but includes only five specimens with complete boreholes (Fig. 3). However, a size refuge from naticid predation does exist for *A. ovalis* for four of five samples (Table 2, Fig. 4). Although *A. ovalis* attained a maximum length of 53 mm, no specimen larger than 37 mm dorsal-ventrally has a complete borehole in any sample (Fig. 4). The disparity

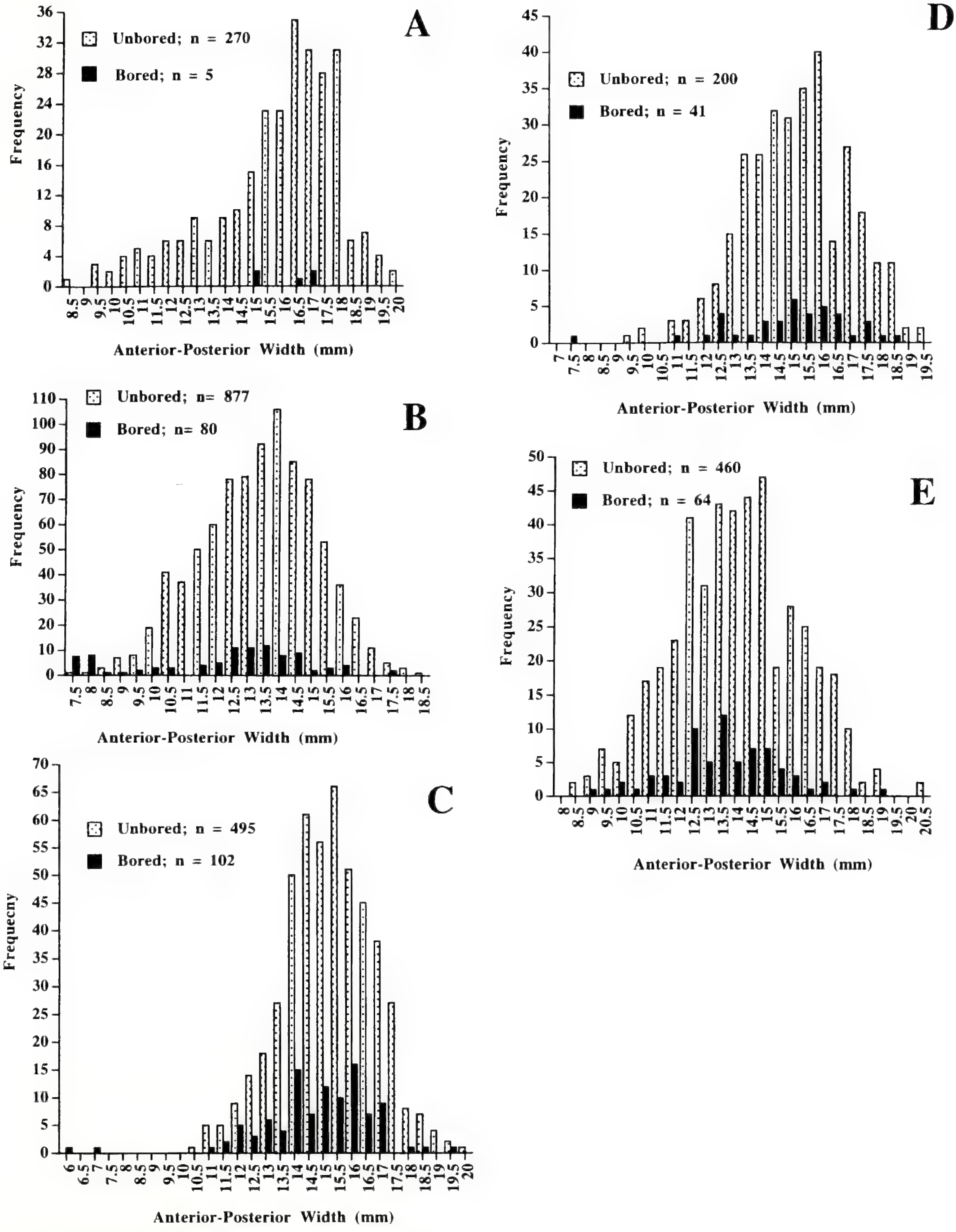


Fig. 3. Size (width)- frequency distribution for bored (black) vs. unbored (stippled) valves of *Divalinga quadrisulcata* for each sampling locality. Locality A, Stone Harbor, New Jersey; B, Kill Devil Hills, North Carolina; C, Wrightsville Beach, North Carolina; D, Litchfield Beach, South Carolina; E, Bahia Honda Beach, Florida.

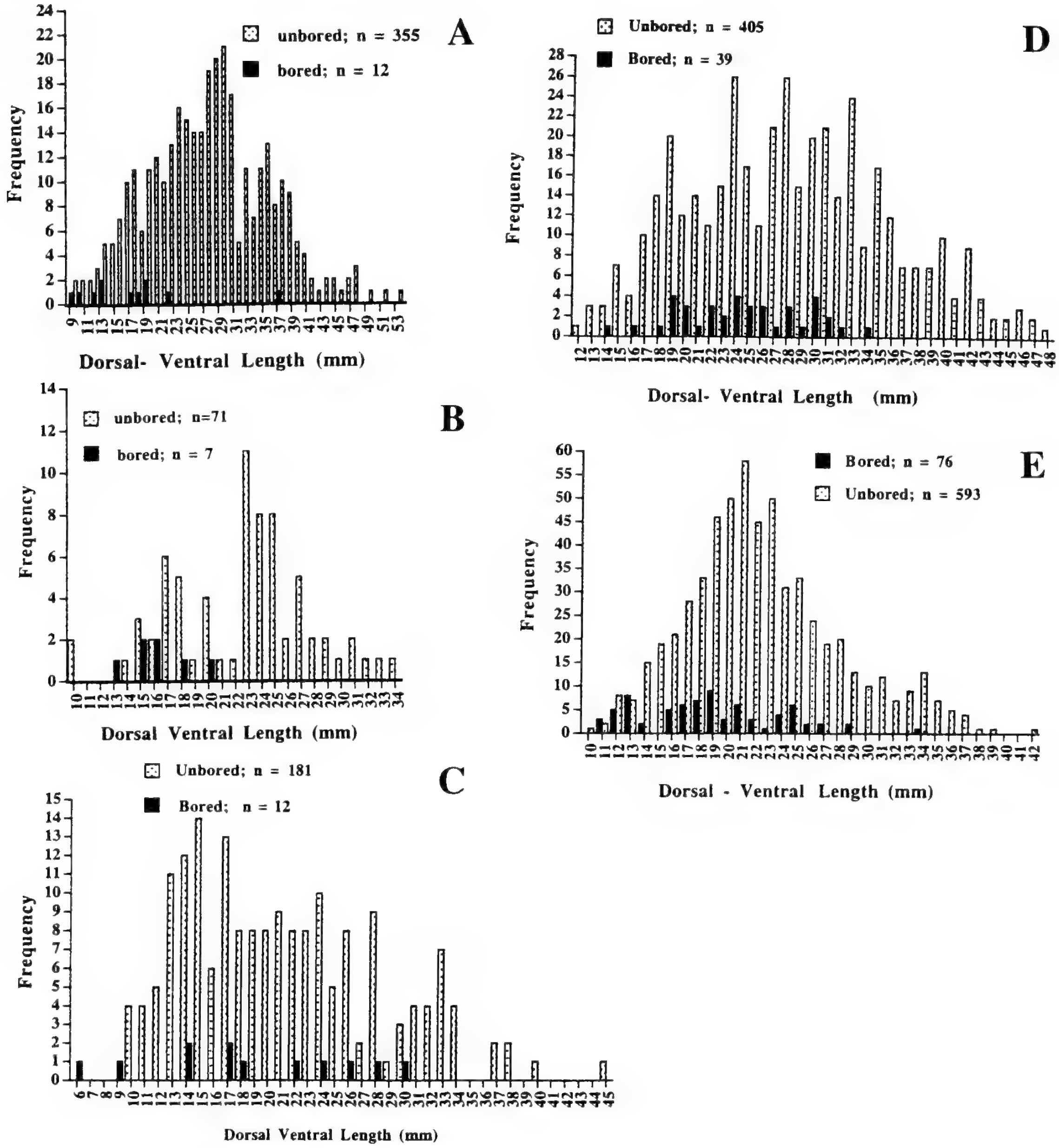


Fig. 4. Size (length)- frequency distribution for bored (black) vs. unbored (stippled) valves of *A. ovalis* for each sampling locality. Locality A, Stone Harbor, New Jersey; B, First Landing State Park, Virginia; C, Kill Devil Hills, North Carolina; D, Wrightsville Beach, North Carolina; E, Huntington Beach, South Carolina.

between largest unbored vs. completely bored specimen averages 14 mm for five samples (Fig. 4).

No correlation exists between the size of the naticid and size of the *Divalinga quadrisulcata* that it drilled for four of the five samples. The r value for regression of OBD on valve width is statistically significant only for *D. quadrisulcata* from NC-W (r = 0.34; Fig. 5; Table 1; Bonferroni test of compared r values). Two of the six samples of *Anadara ovalis* display a significant correlation between OBD and prey valve length (Fig. 5; Table 2; Bonferroni test of compared r values), an indication of prey size-selectivity by the naticids in some prey populations. Interestingly, r values are higher for *A. ovalis* versus *D. quadrisulcata* at all localities (Table 1 vs. 2) where both clam species were sampled. However, no latitudinal trend in size-selectivity is apparent for the blood ark or cross-hatched lucine.

Prey effectiveness (PE) differs drastically among the samples of *Divalinga quadrisulcata* (0.0 to 0.62; Table 1), but less so for *Anadara ovalis* (0.01 to 0.14; Table 2). Excluding the NJ sample (PE = 0.62) due to a small number of bored valves, the disparity in PE remains appreciable for the cross-hatched lucine from North Carolina to the Florida Keys. The FL-K sample has twice the number of incomplete/ nonfunctional boreholes (14) as any other sample (Table 1), save the NJ sample. Prey effectiveness is much less variable among the samples of *A. ovalis* (Table 2) relative to *D. quadrisulcata* (Table 1) due to the fact that the maximum number of valves of blood arks with incomplete boreholes in any sample is three. Eschewing possible taphonomic complications with predation intensity (PI) (see discussion), both clam species show increasing frequency of completely bored valves from NJ to FL (Table 1 and 2). Thus the likelihood that an individual will be successfully drilled by a naticid (PI) increases from the northern to the southern populations of both prey species.

DISCUSSION

Latitudinal trends in naticid-bivalve prey interactions from the Virginian Subprovince to the Caribbean Province are apparent for borehole-site stereotypy, prey effectiveness by (PE), and predation intensity (PI) on *Divalinga quadrisulcata* (Table 1). In contrast, only PI shows a latitudinal trend for naticid predation on *Anadara ovalis*. Borehole-site selectivity on *A. ovalis* remains fixed on the beak area of the valve. Few incompletes are found on valves of blood arks from NJ to FL (Fig. 2). Distinctions in these indices of predation between the two prey species from north to south along the Atlantic Coast may reflect differences in size, ornamentation, and habit between the two bivalve prey, in concert with changes in the dominant naticid predator, and their modal size, at different latitudes.

Bottjer and Carter (1980) stated that the hairy periostracum covering arcids may deter borers. However, the hairy periostracum does not invariably deter naticids from drilling perisotracum-veneered arcid umbos, as evidenced by observations that *Noetia duplicata* could drill the periostracum covered beaks of *N. ponderosa* from North Carolina. Naticid species at all sampled latitudes drilled the exposed umbos of *Anadara ovalis*, either with or without the periostracum abraded (Fig. 2). Invariant stereotypy across molluscan (sub)provinces suggests a convergence of manipulative strategies on the blood ark by the enveloping foot of all naticid species at all latitudes. The ubiquitous semi-infaunal habit may have constrained borehole-site selection on the dorsal portion of the valves of the blood ark just as the semi-infaunal mode of life of *Spisula solidissima* may have conditioned borehole stereotypy on surfclams (Dietl and Alexander, 1997).

In contrast, moonsnails forage for *Divalinga quadrisulcata* beneath the surface, and some naticids are faster burrowers than others (Trueman and Brown, 1992). Foot size differs among naticid species, which could influence manipulation of the prey (Carriker, 1981; Kabat, 1990a). The fact that valves of the cross-hatched lucine have boreholes with the same mean size diameter concentrated in the dorsal area in the SC and FL-K samples as conspecifics from tropical Brazil (Couto, 1996) suggests a similar size predator in each latitude. *Polinices hepaticus* in Brazil (Couto, 1996) and *Naticarius canrena* and *P. lacteus* in the Florida Keys are comparable in size (Abbott and Dance, 1983).

But in populations in temperate latitudes of NC and further north, borehole site selectivity is shifted to the ventral margin of the cross-hatched lucine (Table 1). This latitudinal shift in borehole position may indicate a different naticid predator drilling *Divaricella quadrisulcata* in the northern latitudes of the Carolinian Province. Supporting evidence for a change in the dominant naticid predatory species on *D. quadrisulcata* is found in the significant increase (ANOVA) in the mean OBD in drilled valves in NC vs. the FL-K samples (Table 1). *Sinum perspectivum*, which is very abundant in the North Carolina molluscan assemblages, has a much larger, non-retractable foot, than does either *Naticarius canrena* or *Polinices lacteus*, which abound in the Florida Keys. The significantly smaller mean OBD in the valves of *D. quadrisulcata* from the FL-K sample vs. the NC samples corresponds with the smaller apertural opening of *N. canrena* vs. *S. perspectivum*. Unfortunately, direct observational evidence of either naticid preying on *D. quadrisulcata* is lacking. In the absence of evidence of a change in habit or morphology of the bivalve prey with latitude, however, replacement of the dominant naticid preying on *D. quadrisulcata* in different latitudes is the likely explanation for the shift in borehole-site stereotypy from north to south along the U. S. Atlantic Coast.

In the Virginian Subprovince north of the Delaware Bay where *Neverita duplicata* and *Euspira heros* dominate (Fig. 1), boreholes in the cross-hatched lucine, although few, are located away from the dorsal margin (Fig. 2). In contrast, the lobed and northern moonsnail overwhelmingly concentrate their boreholes on the dorsal area of *Spisula solidissima* (Dietl and Alexander, 1997). Unlike *Divalinga quadrisulcata*, ventral boreholes are invariably incomplete in adults of *S. solidissima* (Dietl and Alexander, 1997). The largest OBD in the NJ sample of *D. quadrisulcata* is 4 mm (Fig. 5), whereas OBDs in *S. solidissima* may be up to 8 mm (Dietl and Alexander, 1997). Maturing lobed or northern moonsnails prefer larger prey species such as *S. solidissima, Anadara ovalis*, *Mercenaria mercenaria* (Linnaeus, 1758), and *Pitar morrhuanus* (Linsley, 1848) for cost-

Table 2. Characteristics of naticid predator-*Anadara ovalis* prey interaction at each locality

Index of Predation	Stone Harbor (SH), NJ	First Landing St. Park (FLSP), VA	Kill Devil Hills (KDH), NC	Wrightsville Beach (WB), NC	Litchfield Beach (LB), SC	Cocoa Beach (CB) , FL
Borehole Site Selectivity[1]	Preference for beak, but statistically unconfirmed	Preference for beak, but statistically unconfirmed	Preference for beak, but statistically unconfirmed	Preference for beak; Chi Square = 957; $p < 0.001$	Preference for beak; Chi Square = 1549; $p < 0.001$	Preference for beak, Chi Square = 40.7 $p < 0.001$
Prey size-class preference & size refuge[2]	Dmax = 0.63 ($p < 0 .001$) Reject Ho that bored= unbored distribution; size refuge	Dmax = 0.66 ($p < 0.008$) Reject Ho that bored=unbored distribution; size refuge	Dmax = 0.20 ($p > 0.83$) Accept Ho that bored = unbored distribution	Dmax = 0.28 ($p < 0.008$) Reject Ho that bored=unbored distribution; size refuge	Dmax = 0.30 ($p < 0.001$) Reject Ho that bored=unbored distribution; size refuge	Undetermined Unbored shells not sampled
Mean DV length of drilled valves	17 mm n = 12 < WB, < CB	16 mm n = 7 < WB, < CB	19 mm n = 12 < WB, < CB	26 mm n = 124 > SH, > FLSP, > KDH, > LB, < CB	17 mm n = 219 < WB, < CB	30 mm n = 40 > all other samples
Mean outer borehole diameter	2.5 mm* n = 12 < WB, < CB	2.7 mm* n = 7 < CB	2.3 mm* n = 12 n = 12 < CB	3.0 mm* n = 124 > SH, > KDH, > LB, < CB	2.8 mm* n = 219 > KDH, <WB, < CB	3.4 mm* n = 40 > all other samples
Mean DV length of unbored valves	27 mm n = 355 >FLSP, > KDH, < WB, > LB	23 mm n = 71 <SH, < WB,	22 mm n = 181 < SH, < WB,	28 mm n = 405 > SH, > FLSP > KDH	22 mm n = 593 < SH, < WB	Not sampled
Predator-prey size correlation[3]	r = 0123 $p > 0.70$ n = 12	r = 0.498 $p > 0.25$ n = 7	r = 0.242 $p > 0.47$ n = 12	r = 0.644** $p < 0.01$ n = 124	r = 0.598** $P < 0.01$ n = 219	r =0.216 $p > 0.15$ n = 40
Prey Efficiency (PE)[4]	PE = 0.08 1/12	PE = 0.14 1/7	PE = 0.08 1/12	PE = 0.02 3/124	PE = 0.01 3/219	PE = 0.02 1/40
Predation Intensity (PI)[5]	PI = 0.06 11(x2)/367	PI = 0.15 6(x2)/78	PI = 0.11 11(x2)/193	PI = 0.18 39(x2)/444[6]	PI = 0.22 74(x2)/ 667[6]	PI = ? (biased sample of only bored valves)

* Statistically significant at $p < 0.05$ in ANOVA. Significant comparisons of means by Fisher PLSD test indicated by < or > ; ** statistically significant r at $p < 0.05$; 1 - Confirmed by Goodness of fit for sectorized data (Fig. 2); 2 - Kolmogorov Smirnov test; 3 - Regression of outer borehole diameter on valve length; 4 - PE calculated as ratio of incomplete and nonfunctional boreholes to total attempts; 5 - PI calculated as twice the number of completely bored valves divided by total number of valves (After Vermeij, 1980) 6 - Based on unbiased second sample of bored and unbored shells from same or immediately proximal locality.

effectiveness and overwhelmingly drill the dorsal area of these semi-infaunal and shallow infaunal clams (Kitchell *et al.*, 1981). Adult moonsnails that forage for these other, larger, semi-infaunal and shallow infaunal species may have preyed on the *D. quadrisulcata* as juveniles.

Mean OBD is significantly larger in the valves of *Anadara ovalis* vs. *Divalinga quadrisulcata* at all sampled localities (Table 1 vs. 2). This substantial difference suggests that either differing species of naticids are preying on each bivalve species, or at least different cohorts (age-classes) of the same moonsnail species are selecting different clam species to drill at each latitude. The mean size of the naticid predator on *A. ovalis* does increase significantly southward from NJ to FL as indexed by the increase in OBD (2.5 to 3.4 mm), but the range of OBDs are easily within the diameters of boreholes that can be created by a single species such as *Neverita duplicata* (Dietl and Alexander, 1997). *N. duplicata* overlaps the entire range of *A. ovalis* samples from NJ to FL-C, but such coincidence does not preclude other naticids from preying on blood arks in the Carolinian Province.

Barring inadequate sample size, the lack of significant correlation between predator-prey size-preference for most of the samples of *Divalinga quadrisulcata*

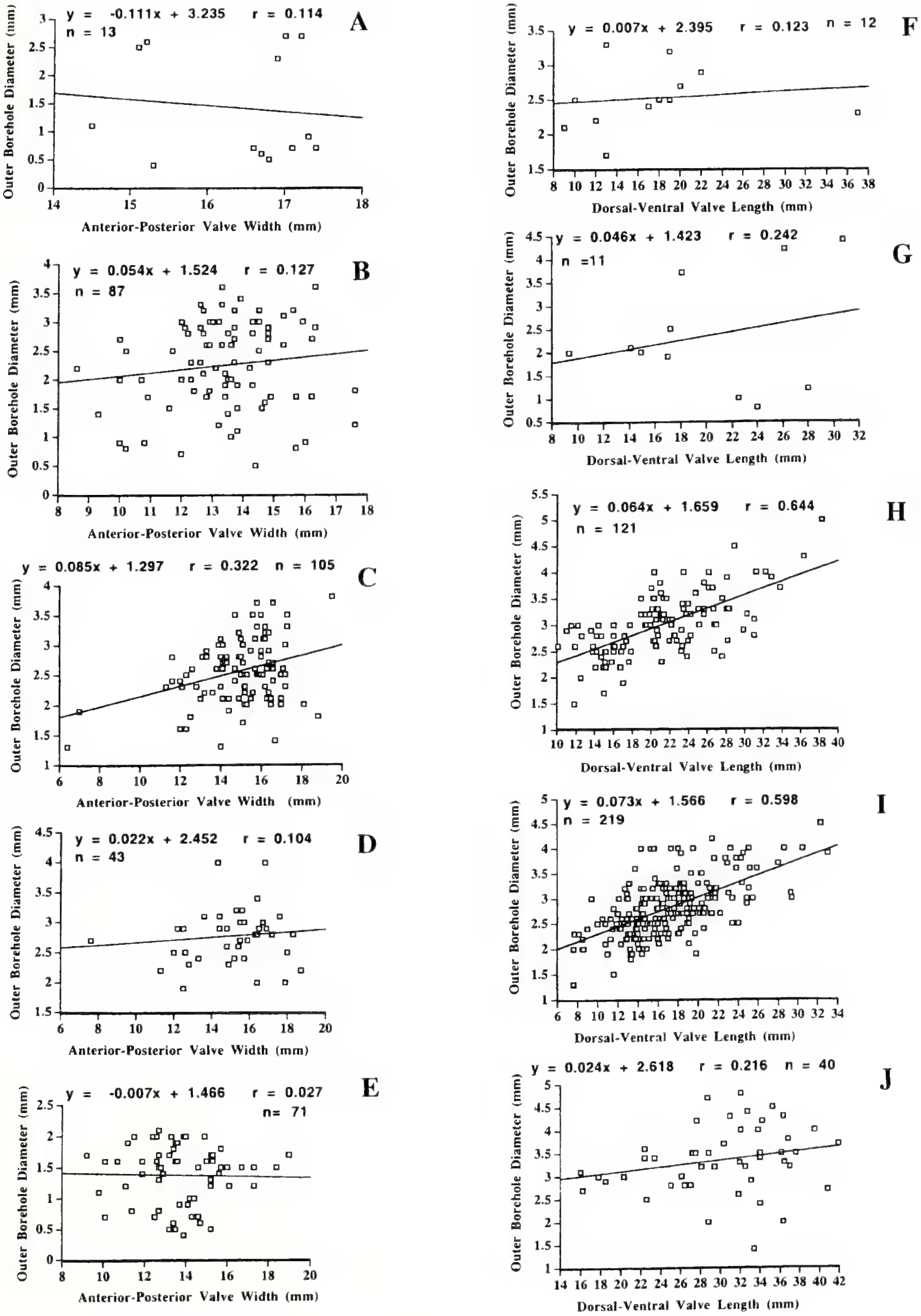


Fig. 5. Regression of outer borehole diameter (OBD) for complete and incomplete boreholes on valve anterior-posterior width of *Divalinga quadrisulcata* and dorsal-ventral valve length of *Anadara ovalis* at each sampling locality. Sample A-E, *D. quadrisulcata*; sample F-J, *A. ovalis*; A & F, Stone Harbor, New Jersey; B & G, Kill Devil Hills, North Carolina; C & H, Wrightsville Beach, North Carolina; D & I, Litchfield Beach, South Carolina; E, Bahia Honda Beach, Florida; J, Cocoa Beach, Florida.

(Fig. 5; Table 1) and *Anadara ovalis* (Fig. 5; Table 2) suggests common mismatches between predator size and prey size. The 1- r^2 values in the regressions of OBD on prey size ranges from 0.999 to 0.889 for *D. quadrisulcata* and 0.98 to 0.59 for *A. ovalis* (Tables 1 and 2). Kitchell *et al.* (1981) documented a correlation of r = 0.63 for *Neverita duplicata* preying on *A. ovalis* from the Georgia Coast (1-r^2 = 0.60). The values indicate the degree of variation in OBD that is not accounted for by corresponding increases in prey size. In biological terms, numerous oversized and undersized predators, relative to the prey size, are apparent in the regressions of OBD on valve length or width (Fig. 5). Although predator-prey size correlation was noted by Couto (1996) for *Polinices hepaticus* preying on *D. quadrisulcata* in Brazil, only the NC-W sample shows statistically significant correlation (r = 0.334) involving naticids preying on the cross-hatched lucine (Table 1). Couto (1996) also mentioned that *D. quadrisulcata* attains a mechanical refuge from predation by *P. hepaticus*, but a size refuge from predation is not statistically substantiated for samples of the cross-hatched lucine along the Atlantic Coast of the U. S., even though sample sizes are large (Table 1; Figs. 3). The largest bored valves are within one mm of the largest unbored valves at any site, except NJ where the sample of completely drilled specimens is small (n = 5) (Fig. 3).

Although the correlation between predator and prey size improves slightly for *Anadara ovalis* relative to *Divalinga quadrisulcata*, no latitudinal trend in prey size-selectivity is apparent in this species either (Table 2, Fig. 5). But a size refuge from naticid predation is attained by *A. ovalis* at four of the five localities (Fig. 4). However, no latitudinal trend in the threshold of the size refuge from predation is evident for *A. ovalis* (Fig. 4). The upper limit of the size (DV length) of bored valves of *A. ovalis* is 37 mm in NJ, and that threshold doesn't increase or decrease southward (Fig. 4), although Kitchell *et al.* (1981) experimentally demonstrated a slightly larger size refuge (AP width = 52 mm; associated DV is ca 42 mm) from naticids preying on *A. ovalis* collected from Georgia. This stasis in "size refugia" from naticid predation is an enigma considering that the mean OBD in valves of the blood ark increases significantly (ANOVA) from 2.5 mm to 3.4 mm from NJ to FL-C (Table 2). It would be expected that the largest bored specimen would increase as the size of the naticid predator increased, based on the increase in mean OBD southward along the Atlantic Coast (Table 2). Regardless of which species and size of naticid are making the predatory attempt, they are unable to manipulate successfully any blood ark after the potential prey reaches a certain size, i.e., 37 mm DV length, whether in NJ or FL.

The latitudinal increase in PE in *Divalinga quadrisulcata* could reflect the decreasing pedal mass of the dominant naticid predator on this bivalve from NJ to FL. The inverse relationship between mean OBD and PE (Fig. 6) supports this possibility. Mean valve size of the cross-hatched lucine actually decreased slightly from the NJ to FL-K samples (Table 1), and the corresponding thickness of these invariantly thin valves did not increase. If the escape potential of the prey increased, it is probably due to a southward reduction in foot size of the dominant naticid species rather than to a change in prey morphology. *Naticarius canrena*, which most likely depredated the FL-K sample, has a smaller foot in comparison to that of *Neverita duplicata* and *Sinum perspectivum*, which affected more northerly populations of *D. quadrisulcata* (Fig. 1). Not surprisingly, *N. canrena* left the smallest borehole on average among the five samples of *D. quadrisulcata* (Table 1). Conceivably, the smaller foot of *N. canrena* allowed *D. quadrisulcata* to escape more often than it did in encounters with higher latitude, larger naticid species with a larger adult foot (Kitchell *et al.*, 1981) (Fig. 1). Hence the number of unsuccessful predatory attempts (incomplete boreholes) increases toward the Caribbean Province for the cross-hatched lucine (Table 1) as the size of the naticid predator decreases (Fig. 6).

PE for *Anadara ovalis* remains low in comparison to *Divalinga quadrisulcata* (Table 1 vs 2), which is initially counterintuitive. *A. ovalis* is six times thicker than *D. quadrisulcata* at the ventral margin. If naticid drilling time is correlated with valve thickness (Kitchell *et al.*, 1981), the former species should experience comparatively longer opportunities for disruption of the drilling event and failure of the moonsnail to penetrate the valve. The unpredictable results for *A. ovalis* could be due to the differences in habit of the two bivalve prey species. *A. ovalis* is a much slower burrower (Alexander, 1993) than is *D. quadrisulcata* (Stanley, 1970). The blood ark probably cannot easily escape a moonsnail that has enveloped it. Although naticids drag their enveloped bivalve prey beneath the sediment surface to bore the clam shell (Kabat, 1990a), moonsnails do not have to burrow after a semi-infaunal blood ark to capture it. In contrast, a moonsnail must often burrow to depths of 20 cm to capture the cross-hatched lucine (Stanley, 1970), which occasionally escaped envelopment by the foot of the pursuing predator. Nevertheless, the PE for *A. ovalis* does show the same inverse relationship, although statistically not significant, with mean size (OBD) of the prevailing naticids as discussed above for *D. quadrisulcata* (Fig. 6).

The increase in predation intensity (PI) from the NJ to the FL samples for *Divalinga quadrisulcata* (Tables 1) suggests that: (1) density of naticids preying on the cross-hatched lucine is increasing southward, (2) alternative bivalve prey species are less cost-effective to drill in southern latitudes, and/or (3) predators are drilling prey faster

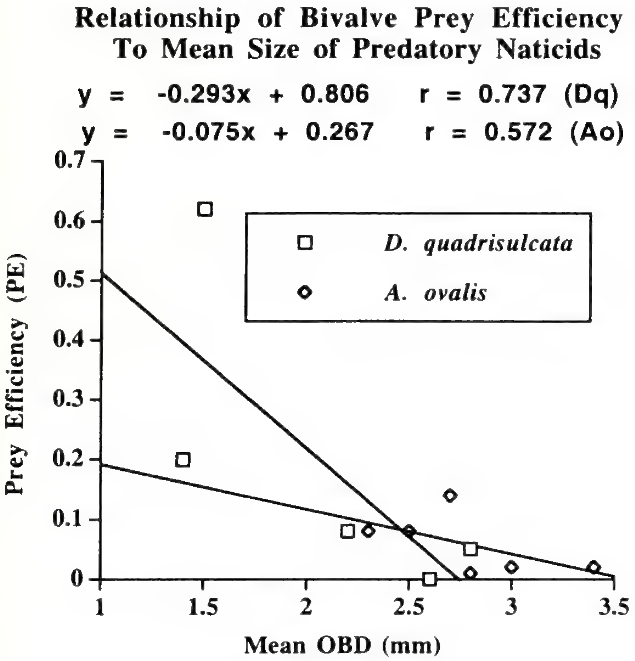


Fig. 6. Relationship between bivalve prey effectiveness (PE) and mean size of predatory naticids for all sample sites of *Anadara ovalis* and *Divalinga quadrsulcata*. r values are not statistically significant.

due to higher ambient temperatures (Q 10 rule) and are therefore capable of consuming more prey per unit time. The preferred prey of naticids in NJ latitudes is *Spisula solidissima* (Dietl and Alexander, 1997), even at very small size (Weissberger, 1999). Relative to *S. solidissima*, orders of magnitude fewer bored valves of *Anadara ovalis, Astarte castana* (Say, 1822), *Geukensia demissa* (Dillwyn, 1817), *Mercenaria mercenaria, Mya arenaria* (Linnaeus, 1758), *Mytlus edulis* (Linnaeus, 1758), *Pitar morrhuanus* (Linsley, 1848), *Pandora gouldiana* (Dall, 1886), and *Petricola pholadiformis* (Lamarck, 1818) have been collected by the authors in NJ (Fig. 1). Kitchell *et al.* (1981) experimentally documented the cost-benefit ratio of naticid predation on varying sized *M. mercenaria* and *M. arenaria*. Smaller bivalves, like *D. quadrisulcata*, are less cost-effective to bore and therefore are less preferred alternative prey. Reinforcing this contention, thousands of specimens of *Donax variabilis* (Say, 1822) examined by the authors show that the species is very infrequently drilled by naticids in NJ. The situation changes in the transition from the Virginian Subprovince to the Carolinian Province. In NC, both *D. variabilis* and *Mulina lateralis* (Say, 1822), another small clam like *D. quadrisulcata* (Fig. 1), are frequently found bored in the same assemblages with the cross-hatched lucine (Alexander, pers. obs.). Although data are not yet quantified, the obvious greater frequency of bored valves of *D. variabilis* in NC relative to NJ indicates that PI on small bivalve species, including *D. quadrisulcata*, is increasing in southern latitudes.

This increase in PI on small clams could result from a shift to these less cost-effective small clams as the once copious supply of surfclams, preferred in northern latitudes, dwindles southward (Fig. 1). Additionally, smaller naticid predators, such as *Sinum perspectivum, Polinices lacteus*, and *Naticarius canrena* (Fig. 1) that appear in the in the Carolinian and Caribbean Province, may select smaller bivalve prey such as *D. quadrisulcata* and *D. variabilis*, unlike *Neverita duplicata* in northern latitudes. Thus the increase in PI on *D. quadrisulcata* southward along the Atlantic Coast probably reflects a shift by naticids to include smaller bivalve prey. The preferred larger prey species, *i. e., Mya arenaria* off Massachusetts (Edwards, 1974) and *Spisula solidissima* off Long Island (Franz, 1977; Dietl and Alexander, 1997) of northern latitudes disappear or become smaller, less abundant in lower latitudes (Fig. 1). Ansell (1982) noted that where the size range of prey is limited and only small prey are available, the increase in demand for food by the naticid is compensated by increase in the rate of predation.

Furthermore, the increased PI could reflect increased ambient temperature southward. Predators drill prey faster due to higher temperatures (Q 10 rule) and are therefore capable of consuming more prey. Ansell (1982) stated that predation rates by naticids are largely dependent on metabolic rates and that increased rates of predation (= increased PI) can be expected in higher temperatures regimes.

The parallelism in their southward increase in PI suggests that both the blood ark and the cross-hatched lucine (Table 1, 2) may have become preferred alternative bivalve prey as surfclams become smaller (replaced by subspecies *Spisula solidissima similis* (Say, 1822)) and less common southward into the Carolinian Province. This southward increase in PI for both *A. ovalis* and *D. quadrisulcata* contrasts with the results of Hansen and Kelley (1995) who documented an equatorward decrease in drilling frequencies in molluscan assemblages (bivalves and gastropods) from the Eocene Cook Mountain interval in Virginia and the Gulf Coast. Vermeij *et al.* (1989) also found a decrease in drilling frequencies toward the tropics for bivalves. They reasoned that slow modes of predation, such as drilling, should decline in importance toward the tropics because of increased mortality risk while handling prey. Similar to our data, Allmon *et al.* (1990) found an increase in drilling frequencies in Cretaceous to Recent turritelline gastropods from lower latitudes, as did Dudley and Vermeij (1978) for Recent turritellids.

The trend of increasing drilling frequencies in *Anadara ovalis* and *Divalinga quadrisulcata* southward is the first to be documented for specific bivalve species. In contrast, for gastropods, Jones *et al.* (1998) documented lower drilling frequencies in the Cretaceous naticid *Euspira rectilabrum* (Conrad, 1858) from the Gulf Coast Ripley Formation relative to The Fox Hills Formation of North Dakota. These data argue against extrapolation of generalizations concerning the biogeography and intensity of drilling predation for all taxonomic groups (gastropods vs. bivalves) or levels (species vs. class). Although trends at the molluscan assemblage level show equatorward decreases in PI (e.g., Hansen and Kelley, 1995), these trends are composite estimates of drilling frequencies for all species, which when examined individually are likely to exhibit species-specific variability as to the latitudinal direction in which their respective PI decreases. Trends in predation intensity at the species level may be attuned to such interaction-related variables as alternative prey species size and abundance. Predation intensity on *A. ovalis* and *D. quadrisulcata* is inversely related to maximum size of alternative bivalve prey (Fig.1), which increases northward, where large *S. solidissima* are drilled preferentially (Dietl and Alexander, 1997).

Relative abundance of a preferred alternative prey may be a controlling influence on the intensity of drilling on a less desirable prey. In "prey switching" (Murdoch, 1969), a predator (in this case a naticid) concentrates a disproportional fraction of its attack potential upon the more abundant species (in this case the surfclam) and might correspondingly spare the less common species (in this case the cross-hatched lucine or the blood ark). As preferred prey become rarer and the naticid search time increases, the moonsnail would switch to more abundant prey where the ratio of energy gained to time spent foraging is more favorable. As the relative abundances of the preferred and non-preferred prey species change inversely across latitude, the predator might then alter its diet so as to concentrate on the now more profitable alternative prey where it becomes the more abundant prey. Accordingly, PI for the most common species whose highest abundances occur in northern latitudes (= *Spisula solidissima*) is expected to decrease toward subtropical latitudes. Likewise, confamilial predation on naticids would increase northward (Jones *et al.*, 1998) as abundance of large-sized moonsnails (= *Euspira heros*, *Neverita duplicata*) increases (Dietl and Alexander, 1995). Thus inverse relationships in latitudinal trends in PI among different bivalve and gastropod prey taxa, including confamilial prey, are predictable if prey switching is a common foraging behavior across latitudes.

A complication in the determination of both PE and PI is the potential differential transport and sorting of bored vs. unbored valves onto the shore (Lever, 1961). If bored valves are placed in the traction load at a lower competent velocity than unbored valves, their numbers stranded higher on the shore may be disproportional to their percent-frequency in the original subtidal population. The consequence would be an inflated PI and possibly a deflated PE. However, Kaplan and Baumiller (2000) demonstrated in flume experiments on models of disarticulated valves of the small brachiopod *Onniella meeki* that condition of the modeled valve, bored or unbored, did not significantly change their respective entrainment in a unidirectional current. The thin ovate, convex brachiopod valve is very similar in size and architecture to the equi-biconvex valves of the clam *Divalinga quadrisulcata*, except that the former is finely radially ribbed and the latter has a fine divaricate ornamentation. By hydrodynamic analogy, bored and unbored valves of the cross-hatched lucine may not be selectively transported.

Valves with a borehole may be more prone to fragmentation than unbored valves of equal size if the borehole acts as a site for initiation of fractures during saltation of the valves (Roy *et al.*, 1994; Hagstrom *et al.*, 1996; Zuschin and Stanton, 1999). If so, reported PI values could be conservative estimates of actual predation intensity. Although both selective fragmentation and/or transport of bored valves might tend to decrease, or increase, the PI values across latitudes, such processes would probably not reverse a latitudinal trend for any species. It is unlikely that an apparent southward increase in PI (Table 1, 2) is in actuality a decrease for these two species, although rate of increase southward could be distorted. Nevertheless, values of PI and possibly PE should not be interpreted too precisely for any bivalve species, however robust a latitudinal pattern might be.

Taphonomic processes are unlikely, however, to bias procedures that utilize only bored valves. Determinations of borehole-site stereotypy by the sectorization method (Fig. 2), and predator-prey size correlation by regression of OBD on shell length (Fig. 5 and 6) are probably independent of biases due to valve-sorting on the shore or fragmentation of the valves facilitated by boreholes. Thus latitudinal trends in borehole site stereotypy on the valves or predator-prey size selectivity are reliable biological indices little affected by taphonomic processes. Furthermore, elucidation of any "size refugia" from predation in a comparison of the length of unbored vs. bored valves (Figs. 3 and 4) is less obfuscated than PE or PI by taphonomic processes. Distortion of PE and PI values involve disproportionate frequencies of bored or unbored valves in samples relative to the parent populations. In contrast, presence/absence of bored or unbored size classes, not frequencies of specimens therein, determines the threshold of a size refuge from predation.

CONCLUSIONS

Borehole-site selectivity shifts from dominantly ventrally located to predominantly dorsally positioned on valves of *Divalinga quadrisulcata* from New Jersey to the Florida Keys, a change attributed to the different naticids affecting northern *(Euspira heros, Neverita duplicata)* vs. southern *(Sinum perspectivum, Polinices lacteus*, and *Naticarius canrena)* populations of the cross-hatched lucine. No such latitudinal shift in stereotypy is evident for *Anadara ovalis* as complete boreholes are rarely situated anywhere but on the umbos of the blood ark at any latitude. No latitudinal change is apparent in the size refuge from predation for either species. No threshold from predation exists for *D. quadrisulcata* as the largest size classes are bored at each sample site. For *A. ovalis*, a size refuge is suggested at each locality. Predator-prey size selectivity shows no pattern from NJ to FL for either species. Correlations between predator and prey size are significant for only a few samples, although the regression coefficients are invariably higher for the blood ark at localities where it was sampled along with the cross-hatched lucine. Prey effectiveness (PE) increases for *D. quadrisulcata* from north to south, suggesting that the smaller southern naticids allow for more frequent interruptions of the drilling process and escape of the prey. Incomplete boreholes are very infrequent on *A. ovalis*, which is a sluggish semi-infaunal burrower, unable to elude the enveloping foot of the naticid predator. Predation intensity (PI) increases for both species from the Virginian to the Caribbean Province, a consequence of the shift to these alternative bivalve prey by naticids that preferred to drill the copious surfclams in the northern latitudes of the Virginian Subprovince. However, taphonomic processes may obfuscate reliability of inferences from PE and PI indices.

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Nutritional studies on soft body and shell of *Achatina fulica* (Pulmonata: Stylommatophora)

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Abstract: The present study is aimed to evaluate the nutritional status of the giant African snail *Achatina fulica* Bowdich. Collected snails were analysed for total weight, weight of whole body soft parts and shell. Soft parts were analysed for biochemical constituents - protein, carbohydrate, and lipid. In addition, a total of 13 elements in both soft parts and shell were estimated. Shell constitutes 22% and soft body 61% of the total weight of the snail, and fluids the remainder, on an average. Biochemical analyses reveal that protein forms 46% (by micro-Kjeldahl method), 56% (by Lowry *et al.* method), carbohydrate 2%, and lipid 12% of dry weight of the entire soft body. Among the metals estimated calcium is the major element in both soft body and shell, consisting of 20% and 25% of total ash respectively. Potassium is the next major element followed by magnesium and sodium in soft body. In the light of present observations, the nutritional status of the giant snail is discussed.

Key Words: *Achatina fulica*, biochemical composition of soft parts, metals of soft parts and shell

Among the microlivestock and unconventional sources of animal proteins, molluscs as a group hold tremendous prospects. In many parts of the world, snails and bivalves occupy a dominant position among the microlivestock that are farmed for food (Vinci *et al.*, 1990). To determine the possibility of using 'snail meal' as a source of animal protein in the feeds of poultry and livestock, assays of essential amino acids were made on the giant African snail *Achatina fulica* Bowdich, a pest of Pacific Islands (Mead and Kemmerer, 1953). The authors observed that arginine is nearly 2.3 times and lysine over 1.3 times the amount present in whole egg and through the addition of snail meal to cottonseed meal and many other vegetable products the deficiency of the essential amino acid lysine could be overcome. Besides, Rees (1950) reports the usage of *A. fulica* including its well-crushed shell for poultry food. Hence it is worthwhile to analyse the composition of both soft body and shell of *A. fulica* to evaluate the nutritional status of the snail. The present study is restricted to a natural population in the Guindy campus of Madras University.

MATERIALS AND METHODS

Specimens of *Achatina fulica* from a natural population in Guindy Campus of Madras University were collected, kept in terraria and starved for a day before analyses to eliminate the gut contents but kept active by sprinkling water. Snails were washed with water to remove the adhering soil and wiped dry before weighing. The shell was carefully removed and the weight of the shell as well as the whole body soft parts were determined separately.

The soft parts were transferred to a preweighed aluminium cup, dried to constant weight in an oven at 80° C, and homogenised.

The total nitrogen content of the soft parts was estimated by micro-Kjeldahl method (Steyermark, 1961). Protein content was estimated by both micro-Kjeldahl and Lowry *et al.* (1951) methods based on an earlier report in this snail (Kalyani and Ramalingam, 1982). 10 % TCA was used as a protein precipitant. The difference in values between estimations of non- protein nitrogen in the TCA supernatant and the total nitrogen was taken as protein nitrogen.

Total carbohydrate was estimated by the anthrone method (Carroll *et al.*, 1956) after digesting the sample in 30 % KOH and precipitating the polysaccharides with ethanol.

Total lipid was estimated by the method of Barnes and Blackstock (1973). Chloroform: methanol (2:1 V/V) was used as the extraction solvent.

To estimate the mineral composition of soft parts and shell of the snail, dried samples of soft parts were incinerated at 600° C for 10 hours and shell at 700° C for 12 hours. A known amount of ash was dissolved in 1 ml of a mixture of concentrated nitric acid and hydrochloric acid (4:1 V/V) and diluted appropriately before analyses. To increase the sensitivity of the analytical procedures, the entire ash content of the soft body was taken for metal analyses in small weight groups of snails.

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Metal concentrations were measured in an ARL 3410 inductively coupled plasma atomic emission spectrophotometer. Metals simultaneously analysed included sodium, potassium, magnesium, calcium, strontium, molybdenum, manganese, iron, copper, zinc, cadmium, and lead in both the soft parts and shell. In addition, cobalt in the soft parts and barium in the shell were estimated.

Total weight of the snails was used as a parameter to classify the collected snails for statistical comparisons as follows: up to 5 g, 5-10 g, 10-20 g, 20-30 g, 30-40 g, 40-50 g, and 50-60 g. A one-way analysis of variance was used to compare the various parameters studied within weight groups as well as between weight groups. The Student Newman - Keuls test as detailed by Sokal and Rohlf (1969) was followed to test for differences among means within the same weight groups or among the weight groups.

RESULTS

A total of 84 snails were collected in the present study and the maximum number of specimens was seen in 20-30 g snails followed by snails up to 5 g. All the absolute values obtained on total weight, shell weight, weight of whole soft body, and dry weight of whole soft body were included for statistical comparisons (Table 1) and the results reveal that the seven groups of snails are significantly distinct in all the weight parameters.

Data obtained on all the biochemical constituents and metals in the soft parts of the snail are presented as percent composition on a dry matter basis. Results reveal that in each weight group protein content is high followed by lipid, and carbohydrate the least (Table 2). However the mean values of the respective biochemical components between the weight groups did not differ significantly. Among the metal content of the soft parts in each weight group calcium is high followed by potassium, magnesium, and sodium; other metals constitute less than 1 % of inorganic content of the soft body (Table 3). Differences observed in the content of all respective metals between different groups are not significant.

Metal analyses of the shell of *Achatina fulica* in seven weight groups are given as percent composition in relation to total shell weight (Table 4). It is not surprising that calcium of shell occurs in significantly higher concentration than the rest of the metals that form less than 1 % of ash content, in each weight group. None of the mean values of the respective metals analysed in the shell showed a significant change among the weight groups.

DISCUSSION

The present investigation on *Achatina fulica* from a population in the Guindy Campus, Madras University indicates that the percent composition of soft body parts decreases with increase in total weight of the snails which includes fluids (haemolymph, mucus, etc.) that are lost

Table 1. Weight composition of *Achatina fulica*. Values (mg) are means ± standard deviation, n = sample size, % = percentage of total weight. Between groups comparison (Student-Newman-Keuls test): Highlighted values are significant at $p < 0.01$.

Weight Group (g)	n	Total Weight	Shell Weight Absolute	Shell Weight %	Weight of whole Soft body Absolute	Weight of whole Soft body %	Dry weight of whole Soft body Absolute	Dry weight of whole Soft body %
0-5	19	1845.34 ±956.08	219.15 ±197.28	11.88	1267.19 ±652.68	68.67	232.13 ±118.27	12.58
5-10	5	7144.00 ±2391.57	1550.00 ±1117.60	21.70	4404.00 ±604.31	61.65	644.80 ±260.02	9.02
10-20	7	16622.54 ±2940.02	3181.42 ±597.06	19.14	10808.25 ±2186.95	65.02	2368.26 ±718.86	14.23
20-30	26	25113.52 ±2573.32	5600.39 ±1392.75	22.51	15913.27 ±2495.35	63.37	3491.18 ±1020.76	13.90
30-40	13	34053.00 ±2807.42	6068.07 ±1436.67	17.82	21616.07 ±1987.80	63.48	4761.16 ±1069.53	13.98
40-50	9	45910.39 ±3481.34	14667.33 ±5380.12	31.95	25022.61 ±2767.26	54.50	4882.64 ±964.80	10.64
50-60	5	57865.75 ±5147.41	18313.00 ±5157.22	31.65	29339.95 ±8317.60	50.70	6353.95 ±1741.27	10.98

Table 2. Biochemical composition of *Achatina fulica*. Components expressed as mg % of dry weight of whole soft body; values are means ± standard deviation, n = sample size; nd = not determined; *not included for statistical analyses. Within group comparison: Highlighted values are significant at p < 0.01. Between groups comparison: All values (including highlighted) are nonsignificant.

Weight Group (g)	Protein		Non protein nitrogen	Carbohydrate	Lipid
	Micro-Kjeldahl method	Lowry *et al.* method			
0-5	39.86	53.99	0.16	1.49	15.31
	±11.99	±10.75	±0.08	±0.87	±2.61
	n=11	n=11	n=4	n=11	n=11
5-10	51.78	57.76		1.00	14.88
	15.77	6.87	nd	0.59	3.35
	n=5	n=5		n=5	n=5
10-20	43.81	66.97	0.13	2.02	11.38
	±6.94	±15.13	±0.07	±0.57	±2.41
	n=7	n=7	n=4	n=7	n=7
20-30	44.90	59.73	0.19	2.57	10.49
	±9.19	±11.95	±0.09	±2.13	±2.78
	n=26	n=26	n=17	n=26	n=26
30-40	43.89	54.91	0.20	2.00	12.18
	±6.47	±13.13	±0.12	±1.21	±3.50
	n=13	n=13	n=8	n=13	n=13
40-50	51.04	51.32	0.23	2.18	11.69
	±6.07	±10.06	±0.12	±0.39	±3.69
	n=9	n=9	n=6	n=9	n=9
50-60	41.44	47.38	0.45*	1.84	9.05
	±16.10	±18.57		±0.74	±3.51
	n=5	n=5	n=1	n=5	n=5

while removing the soft parts from the shell. This fluid component also varies (from 8.14 to 19.84 % of total weight) in the different weight groups analysed.

Among the seven weight groups studied, 20-30 g snails were more numerous and are invariably mature.

Earlier investigation on *Achatina fulica* has shown protein to be the major constituent in the albumen gland and apical uterus with a significant increase in protein content of these glands in the preparatory phase of reproduction compared to that in the spent phase (Ramasubramaniam, 1979a). The present analyses also reveals that protein is the major biochemical constituent in the whole body soft tissues of *A. fulica* in all the weight groups, followed by lipid and carbohydrate.

Metabolism in Stylommatophora seems to be carbohydrate oriented and as a result lipids are not very important as reserves (Voogt, 1983). However the present study on *Achatina fulica* reveals lipid to occur in greater concentration (10 to 15 % dry weight of whole soft body) than carbohydrate.

While evaluating the flesh of *Achatina fulica* as food for fingerlings of *Oreochromis mossambicus* (Peters), Shafiei and Costa (1989) have indicated on a dry matter basis the mean percentages of protein, carbohydrate, and lipid to be 49.6 %, 33.3 %, and 10.7 % respectively. This is in contrast with the present observation on *A. fulica* where carbohydrate content is very low.

The results obtained on ash content of both soft parts and shell reveal that the former has fewer inorganic constituents (Tables 3 and 4) while the latter has the maximum. It is well known that sodium, potassium, magnesium, and calcium occur in large amounts in organisms (Simkiss and Taylor, 1989). This is observed in the present study also: amounts of calcium > potassium > magnesium > sodium in the soft parts of *Achatina fulica*. A similar situation also exists in the shell, though the contents of potassium, sodium, and magnesium are several times less than those of the soft tissues. And, the shell has in addition strontium whose concentration is higher than that of potassium, sodium, and magnesium. According to Reineskog and Peterson (1950) the shell of the snail, in contrast to human bone, is a non-living tissue. However, earlier study on *A. fulica* has shown that the shell is not merely a mineralised exoskeleton but a storage site for calcium to supply this metal needed for egg shell production (Ramasubramaniam, 1979b). It is worthy to note that the differences observed in calcium content of shell between higher weight groups of snails in the present study, although not statistically significant, support this observation. Because elements belonging to the same column of the periodic table resemble each other in their chemical properties (Suzuki *et al.*, 1990), strontium could have accumulated in the shell and soft parts of *A. fulica* following the same metabolic pathway as calcium.

In the case of terrestrial molluscs, dietary sources of metals are presumably of prime importance to the animal and the metal content of many gastropods reflects the concentration of metals on or in their food supply. However, the possibilities of extracellular hormones or intracellular regulatory molecules for these elements are still largely unexplored (Simkiss and Mason, 1983). Although present in very low concentrations, the metals zinc, copper, molybdenum, and manganese are important as they are involved structurally in the formation of metalloenzymes in mollusks. In addition, magnesium is frequently associated with enzymes, though it might not be structurally a part of the molecule (Simkiss and Mason, 1983).

Supporting the studies of Miloslavich (1996), quantification of biochemical substances is relevant as it estimates the amount potentially available from *Achatina fulica* for the nutrition of both human and cultured organisms. The present study further reveals that any weight group of this

Table 3. Metal content of the whole body soft tissues of *Achatina fulica*. Metals are expressed as µg% of dry weight of whole soft body; values are means ± standard deviation; n=sample size. Within group comparison: Highlighted values are significant at $p < 0.01$. Between groups comparison: All values (including highlighted) are nonsignificant.

Weight Group(g)	Ash % of Dry Weight(mg)	Sodium	Potassium	Magnesium	Calcium	Strontium	Molybdenum	Manganese	Iron	Cobalt	Copper	Zinc	Cadmium	Lead
0-5	5.51 ±2.90 n=12	0.53609 ±0.31518 n=5	1.10274 ±0.60245 n=5	0.66941 ±0.45958 n=5	2.35442 ±0.72668 n=3	0.01990 ±0.01571 n=5	0.02183 ±0.01406 n=5	0.01718 ±0.01265 n=5	0.06615 ±0.06571 N=5	0.00076 ±0.00059 n=4	0.01234 ±0.00980 m=5	0.02190 ±0.01654 n=5	0.00226 ±0.00247 n=4	0.03341 ±0.03597 n=4
5-10	9.46 ±1.97 n=5	0.52370 ±0.31620 n=5	1.04350 ±0.65600 n=5	0.58180 ±0.63320 n=5	1.32180 ±0.47860 n=3	0.01430 ±0.01540 n=5	0.02300 ±0.01450 n=5	0.02880 ±0.04420 n=5	0.18470 ±0.24430 N=5	0.00090 ±0.00080 n=5	0.01110 ±0.01210 m=5	0.03030 ±0.02920 n=5	0.00290 ±0.00180 n=4	0.01990 ±0.01060 n=4
10-20	7.08 ±1.07 n=7	0.21258 ±0.14519 n-3	0.71827 ±0.43028 n=3	0.19930 ±0.22057 n=3	0.98334 ±0.02711 n=3	0.58626 ±0.77709 n-3	0.00870 ±0.00063 n=3	0.00686 ±00956 n=3	0.01040 ±0.01295 n=3	0.00015 ±0.00003 n=3	0.00620 ±0.00843 n=3	0.01070 ±0.01080 n=3	0.00078 ±0.00045 n=3	0.00587 ±0.00073 n=3
20-30	6.36 ±1.54 n=26	0.42065 ±0.07793 n=6	0.79679 ±0.24964 n=6	0.58719 ±0.29459 n=6	1.29102 ±0.11568 n=5	0.01218 ±0.00290 n=5	0.00860 ±0.00098 n=5	0.01510 ±0.00545 n=6	0.03837 ±0.02632 n=6	0.00018 ±0.00010 n-5	0.01225 ±0.00390 n=6	0.01611 ±0.00620 n=6	0.00045 ±0.00025 n=5	0.00543 ±0.00365 n=5
30-40	7.05 ±2.11 n=13	0.30083 ±0.16543 n=6	0.70593 ±0.35279 n=6	0.45298 ±0.27724 n=5	0.90888 ±0.17260 n-=3	0.00943 ±0.00651 n=6	0.00907 ±0.00277 n=5	0.01314 ±0.00682 n=6	0.02312 ±0.00465 n=6	0.00017 ±0.00010 n=5	0.01023 ±0.00572 n=6	0.01182 ±0.00734 n=6	0.00065 ±0.00039 n=4	0.00818 ±0.00506 n=4
40-50	7.29 ±2.07 n=9	0.32817 ±0.17878 n=6	0.73863 ±0.37077 n=6	0.59959 ±0.53905 n=5	1.27618 ±0.65551 n=3	0.01117 ±0.00754 n=6	0.00869 ±0.00562 n=5	0.01250 ±0.00815 n=6	0.01823 ±0.01194 n=6	0.00025 ±0.00021 n=5	0.01407 ±0.01224 n=6	0.03545 ±0.03134 n=6	0.00217 ±0.00103 n=4	0.00873 ±0.00368 n=4
50-60	6.29 ±1.56 n=5	0.39040 ±0.31886 n=3	0.67931 ±0.28754 n=3	0.32716 ±0.28741 n=3	0.97063 ±0.04479 n=3	0.01005 ±0.00789 n=3	0.00759 ±0.00221 n=3	0.00805 ±0.00859 n=3	0.02005 ±0.01905 n=3	0.00017 ±0.00010 n=3	0.00843 ±0.00995 n=3	0.02484 ±0.03231 n=3	0.00435 ±0.00426 n=3	0.01185 ±0.00800 n=3

Table 4. Metal content of the shell of *Achatina fulica*. Metals are expressed as µg% of weight of shell; values are means ± standard deviation; n=sample size: for metals n=4 in 0-5g weight group; n=3 in other groups; nd=not determined. Within group comparison: Highlighted values are significant at $p < 0.01$. Between groups comparison: All values (including highlighted) are nonsignificant.

Weight Group(g)	Ash % of Dry Weight(mg)	Sodium	Potassium	Magnesium	Calcium	Strontium	Barium	Molybdenum	Manganese	Iron	Copper	Zinc	Cadmium	Lead
0-5	84.39 ±6.66 n=9	0.06137 ±0.02809	0.01173 ±0.00585	0.05802 ±0.02552	29.05115 ±14.47092	0.08994 ±0.01254	0.01166 ±0.00462	0.00087 ±0.00035	0.00464 ±0.00078	0.02121 ±0.00438	0.00935 ±0.00132	0.00640 ±0.00180	0.00034 ±0.00009	0.02475 ±0.01229
5-10	92.16 ±2.89 n=5	0.06612 ±0.02258	0.04847 ±0.04334	0.02672 ±0.01385	27.74651 ±22.31666	0.14323 ±0.07580	0.00746 ±0.00257	0.00150 ±0.00176	0.00279 ±0.00240	0.01880 ±0.01077	0.00006 ±0.00007	0.00422 ±0.00405	0.00019 ±0.00007	0.01009 ±0.00558
10-20	94.14 ±1.33 n=5	0.05949 ±0.00829	0.00845 ±0.00167	0.03183 ±0.00879	9.11179 ±0.38146	0.09846 ±0.04574	0.00751 ±0.00561	0.00040 ±0.00021	0.00402 ±0.00114	0.01720 ±0.00778	0.01027 ±0.00201	0.00516 ±0.00143	0.00026 ±0.00000	0.01470 ±0.00052
20-30	89.20 ±4.77 n=9	0.05557 ±0.01388	0.02564 ±0.02772	0.02552 ±0.00200	35.35293 ±3.56172	0.09764 ±0.01289	0.00386 ±0.00277	nd	0.00334 ±0.00119	0.01136 ±0.00124	0.00697 ±0.00344	0.00382 ±0.00119	0.00025 ±0.00003	0.01256 ±0.00086
30-40	83.08 ±11.38 n=6	0.05615 ±0.01812	0.03664 ±0.02592	0.02738 ±0.01770	29.66660 ±20.90999	0.08843 ±0.02867	0.00336 ±0.00236	0.00129 ±0.00168	0.00286 ±0.00236	0.00981 ±0.00562	0.00593 ±0.00704	0.00279 ±0.00249	0.00015 ±0.00010	0.00911 ±0.00492
40-50	94.87 ±2.08 n=7	0.05315 ±0.00493	0.02686 ±0.02783	0.02283 ±0.00664	9.19232 ±2.13759	0.10122 ±0.03481	0.00598 ±0.00224	0.00049 ±0.00022	0.00354 ±0.00143	0.01109 ±0.00378	0.00704 ±0.00209	0.00410 ±0.00080	0.00024 ±0.00002	0.01319 ±0.00068
50-60	93.24 ±2.41 n=4	0.05267 ±0.01311	0.03755 ±0.02289	0.02634 ±0.01461	30.28400 ±19.00228	0.12845 ±0.01415	0.00731 ±0.00451	0.00079 ±0.00084	0.00318 ±0.00242	0.01127 ±0.00484	0.00760 ±0.00648	0.00349 ±0.00301	0.00030 ±0.00017	0.01010 ±0.00610

snail is equally nutritionally rich. A parallel study on the fatty acid composition of this snail by the author has shown the foot, the major part of the flesh, to be rich in essential fatty acids, as is the albumen gland, which grows up to one tenth the weight of the soft body in the preparatory phase of reproduction of this snail. It is hoped that the present observations on the nutritional status of this pest-turned-food snail would initiate similar studies in other areas where these snails are widely distributed.

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SYMPOSIUM: BIOMINERALIZATION

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Biomineralization in chiton teeth and its usefulness as a taxonomic character in the genus *Acanthopleura* Guilding, 1829 (Mollusca: Polyplacophora)

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Abstract: The physical structure and mechanisms of biomineralization have been elucidated in the major lateral teeth of the chiton genus *Acanthopleura* with the aid of light and scanning electron microscopy and energy dispersive spectroscopy. Following its recent revision, this genus currently consists of 15 species, including three species suppressed as synonyms. Specimens representing all 18 (nominal) species have been examined. With two exceptions, the major laterals are typically discoid and unicuspid with only limited interspecific variation. The teeth of *A. loochooana* are also essentially discoid but have a small, distinct distal indentation, while those of *A. rehderi* possess four short rounded denticles. Biomineralization in all species of *Acanthopleura* occurs in architecturally discrete compartments and, with the exception of *A. rehderi*, is consistent in all tooth regions except the cusp core, where *A. curtisiana, A. miles, A. araucariana* and *A. loochooana* differ in having substantial amounts of iron. The first three of these species were previously included in the genus *Squamopleura* and there is evidence to suggest that this genus should not have been suppressed. The substantial difference in tooth structure between *A. rehderi,* with its four denticles and total lack of a lepidocrocite region, and that of other members of the genus *Acanthopleura* suggest that this species may be more closely aligned with *Onithochiton*. The inclusion of additional characters, such as tooth biomineralization, is strongly recommended in future studies of chiton taxonomy.

Key Words: Polyplacophora, radula, biomineralization, systematics, magnetite

Chitons are common marine molluscs found in intertidal and subtidal habitats throughout the world where they play a significant role in reef and near-shore ecology, particularly through coastal bioerosion (Kangas and Shepherd, 1984; Kirschvink, 1985; Rasmussen and Frankenberg, 1990). In recent years, the position of chitons in the evolutionary development of the phylum Mollusca has been under considerable debate (see for example: Salvini-Plawen, 1980, 1985; Eernisse, 1984; Scheltema, 1988; Sirenko, 1993; Eernisse and Reynolds, 1994; Buckland-Nicks, 1995). However, while there has been a resurgence of interest in the systematics of the Polyplacophora, the higher classification of this group is still based on traditional gross morphological characters such as the valve architecture, girdle armature and insertion plate detail (Sirenko and Starobogatov, 1977; Van Belle, 1983). It has been suggested that caution should be exercised in the primary use of these traditional characters, with the current belief of many molluscan taxonomists being that an understanding of the true evolutionary development of these organisms can be achieved only through the consideration of as many different characters as possible (Bullock, 1988; Eernisse and Reynolds, 1994; Ponder and Lindberg, 1997).

The Polyplacophoran radula is bilaterally symmetrical around a central rachidian tooth and contains 17 teeth in each row, two of which, the major laterals, are biominerally hardened and have received considerable attention since the discovery that they are impregnated with the iron mineral magnetite (Lowenstam, 1962). Studies have since revealed that they are progressively mineralized along the length of the radula right up to the final working teeth (Macey *et al.*, 1996; Macey and Brooker, 1996), which are capable of abrading the rock substrate to enable feeding on the embedded algae. At least two distinct mineralization strategies are employed by chitons to construct these teeth, resulting in teeth of different composition (Lowenstam and Weiner, 1989; Macey and Brooker, 1996). In one strategy, typified by the genera *Cryptochiton* and *Cryptoplax*, the tricuspid teeth ultimately contain a core of amorphous hydrous ferric phosphate covered in a magnetite cap. In the second, illustrated in the family Chitonidae, the unicuspid teeth have a posterior cap of magnetite, lined by a thin layer of lepidocrocite with a central core composed of dahllite, francolite or fluorine substituted hydroxyapatite (Lowenstam, 1967; Lowenstam and Weiner, 1985; Evans *et al.*, 1992;

Lee *et al.*, 1998). Although recent investigators have recognised the importance of radula tooth morphology in chiton systematics (Ferreira, 1986; Bullock, 1988; Kaas and van Belle, 1985-1994), the variety of mineralization strategies employed by chitons has not to date been recognised as a character that could well reflect phylogenetic affinities.

The chiton genus *Acanthopleura* has recently been revised by Ferreira (1986), who used traditional morphological characters as a basis for including species from the three genera; *Liolophura* Pilsbry, 1893 (type: *Chiton japonicus* Lischke, 1873), *Squamopleura* Nierstrasz, 1905 (type: *Squamopleura imitator* Nierstrasz, 1905), and the monotypic *Enoplochiton* Gray, 1847 (type: *Chiton niger* Barnes, 1824). This revision resulted in the suppression of some species as synonyms and the construction of a genus comprising 15 species, two of which were newly described. This revision has led to some controversy, with the scientific community either apparently reluctant to accept certain aspects of the classification, or exhibiting a preference for established nomenclature (Bullock, 1988; Emam *et al.*, 1992; Strack, 1993; Suzuki *et al.*, 1997). Indeed, several authors have suggested that some suppressed species should have their original species status reinstated (Strack, 1993; Saito and Yoshioka, 1993). As such, the aims of this current study are to determine whether biomineralization in the radula of chitons is of value as a taxonomic character at the species level, and whether it can be utilised in a re-evaluation of the systematics of the genus *Acanthopleura* in particular.

MATERIALS AND METHODS

Wherever possible, specimens of the 18 (nominal) species of the chiton genus *Acanthopleura* were collected fresh from various locations around the world and preserved in 70% ethanol. These were supplemented by the use of formalin-preserved museum specimens. Multiple specimens were analysed if there was either a wide geographic range, or a marked difference in the biomineralization strategy. Two species (*A. testudo* and *A. araucariana*) were available only as formalin-preserved museum specimens. Specimens of *Ischnochiton (Ischnoradsia) australis* (Sowerby, 1840) and *Plaxiphora (Plaxiphora) albida* (Blainville, 1825) were collected, preserved, and included as further representatives of the suborder Chitonina. These species have major lateral teeth that possess two and three denticles respectively, and as such may present alternative biomineralization strategies to that of the unicuspid members of *Acanthopleura*. Preserved specimens of *Onithochiton quercinus* (Gould, 1846) were also included as an outgroup, as several of the species currently assigned to *Acanthopleura* were previously considered to belong to the Liolophurinae of which *Onithochiton* is still a member. In order to avoid problems with any ontogenetic variation (see *e. g.* O'Neill, 1984), a size class representing mature adult specimens within each species was selected for examination. A complete list of all animals used, together with their size and collection site, is given in Table 1.

The radulae were dissected out of the animals and placed between two pieces of glass so that they were kept flat during subsequent processing. In order to correlate the different coloured teeth seen at the light microscope (LM) level with those examined in the scanning electron microscope (SEM), the radulae were examined and photographed at this stage. From this examination it was determined that, although the total number of teeth varied among species, all of the radulae could be divided into four different stages of development. These consisted of clear, unmineralized teeth at the posterior end of the radula, followed by yellow teeth, then orange teeth and finally black magnetite-capped teeth at the anterior end.

For elemental analysis using energy dispersive spectroscopy (EDS), the radulae were cleaned and dehydrated before being processed into resin blocks such that subsequent grinding exposed the major lateral teeth in longitudinal section. Prior to being carbon coated and viewed in a Philips XL20 SEM, the radulae were again examined and photographed at the LM level so that accurate tooth stage determinations could be made. Teeth at different stages of development along the length of the radula were selected for detailed elemental examination using a LINK/ISIS Series 300 analytical system with a germanium window and lithium drifted silicon detector. This system allows for the analysis of all elements with an atomic weight equal to or greater than that of carbon and quantitative analysis was obtained for the elements: C, O, Na, Mg, Al, Si, P, S, Cl, K, Ca, Fe, Cu and Zn. Line scans and spot analyses were undertaken at 20 KeV, at a working distance of 11 mm and magnification of x10,000. The beam current was 7×10^{-2} nA, with an acquisition time of 60 seconds and a specimen tilt of 15°. The EDS system was calibrated at regular intervals using a cobalt standard. High-purity magnetite (Fe_3O_4) was obtained from Johnson Matthey Chemicals. Lepidocrocite (γ-FeOOH) and hematite (α-Fe2O3) standards were synthesised by methods based on those collected together by Schwertmann and Cornell (1991), while hydroxyapatite ($Ca_5(PO_4)_3(OH)$) was prepared by the method of Hayek and Newesely (1963). All standards were characterised by X-ray diffraction and Raman spectroscopy prior to use. Resin blocks, without radulae, were also processed and analyzed together with the sample blocks in order to determine the elements present in the resin.

Examination of provisional X-ray maps and backscattered electron images, together with LM micrographs,

Table 1. Chiton species examined together with their respective collection sites and whole animal dimensions. Genera are *Acanthopleura, Ischnochiton, Plaxiphora,* and *Onithochiton.*

Species	Collection site	Size (mm)
Acanthopleura granulata (Gemlin, 1791)	Florida Keys, Bahamas	58 x 43
A. spinosa (Bruguiére, 1792)	Cape York Peninsula, Qld, Australia	41 x 33
A. testudo (Spengler, 1797)*	Dijbouti, Gulf of Aden[1]	31 x 28
A. echinata (Barnes, 1824)	San Bartolo 50 km south of Lima, Peru	58 x 42
	Quintay, Santiago, Chile	132 x 79
A. nigra (Barnes, 1824)	San Bartolo 50 km south of Lima, Peru	71 x 39
A. gemmata (Blainville, 1825)	Earlando, Whitsunday Coast, Qld, Australia	47 x 34
	Shark Bay, WA, Australia	66 x 49
	Vilanculos, Mozambique, Africa[2]	62 x 52
A. hirtosa (Blainville, 1825)	Woodmans Point, Perth, WA, Australia	32 x 22
A. gaimardi (Blainville, 1825)	Town Beach, Port Macquarrie, NSW, Australia	40 x 24
A. loochooana (Broderip & Sowerby, 1829)	Kadena, Okinawa, Japan	27 x 18
A. brevispinosa (Sowerby, 1840a)	Middle Id, Aldabra, Seychelles[3]	30 x 24
	Aldabra, Seychelles[3]	34 x 25
	Unguja Id, Tanzania, Africa	41 x 29
A. japonica (Lischke, 1873)	Cape d'Aguilar, Hong Kong	25 x 20
A. vaillantii Rochebrune, 1882*	Sinai, Na'ama, Egypt[4]	37 x 26
A. curtisiana (Smith, 1884)	Nickel Bay, Karratha, WA, Australia	21 x 13
	Cape Kerraudren, WA, Australia	20 x13
A. miles (Carpenter in Pilsbry, 1893c)	Barrow Is, Dampier Archipelago, WA, Australia	39 x 15
	Kendrew Is, Dampier Archipelago, WA, Australia[5]	21 x 13
	Ambon, Latuhala, Indonesia[4]	
A. araucariana (Hedley, 1898)	Pine Is, New Caledonia[6]	34 x 21
	Pine Is, New Caledonia[6]	43 x 27
A. tenuispinosa (Leloup, 1939)*	Ikenma, Oshima Strait, Japan	34 x 19
A. arenosa Ferreira, 1986	Trinity Beach, Qld. Australia	21 x 15
	Trinity Beach, Qld. Australia	23 x 16
A. rehderi Ferreira, 1986	Palmerston Id. Cook Is.[7]	24 x 14
	Mauke Id. Cook Is.	27 x 18
Ischnochiton australis (Sowerby, 1840)	Ottway Penninsula, SA, Australia	69 x 41
Plaxiphora albida (Blainville, 1825)	Ottway Penninsula, SA, Australia	62 x 49
Onithochiton quercinus (Gould, 1846)	Armstrong Bay, Rottnest Id. WA, Australia	39 x 23

* Denotes species considered by Ferreira (1986) to be junior synonyms of *Acanthopleura gemmata*

[1] National Natural History Museum of Leiden - catalogue number 23088/HL390110
[2] Natal Museum - uncatalogued specimen
[3] British Museum of Natural History - Acc no 2211
[4] H. L. Strack - private collection
[5] Western Australian Museum - uncatalogued specimen
[6] California Academy of Sciences - CASIZ 076483/1318
[7] Smithsonian Institute National Museum of Natural History - USMN 685399

allowed the transition zones, that is where the mineralization processes changed rapidly, to be identified. In addition, these techniques showed that the major lateral teeth cusps of the majority of *Acanthopleura* species could be divided into five discrete regions. These consisted of a magnetite region that comprises the posterior cutting surface; a lepidocrocite region adjacent and anterior to the magnetite; an anterior apatite region of the cusp; a junction zone separating the tooth cusp from the base of the tooth, and the base itself (Fig. 1). From the X-ray maps it was apparent that biomineralization in the apatite core was not homogeneous, thus for the purpose of EDS analysis two representative areas were selected, namely the central/posterior and the anterior regions (Fig. 1). Spectra were acquired at points in all identified regions in selected teeth along the radula.

SYSTEMATIC TREATMENT

Class Polyplacophora Gray, 1821
Order Neoloricata Bergenhayn, 1955
Suborder Chitonina Thiele, 1931
Family Chitonidae Rafinesque, 1815
Genus *Acanthopleura* Guilding, 1829
Type-species: *Chiton spinosus* Bruguiére, 1792, by subsequent designation (Gray, 1847)

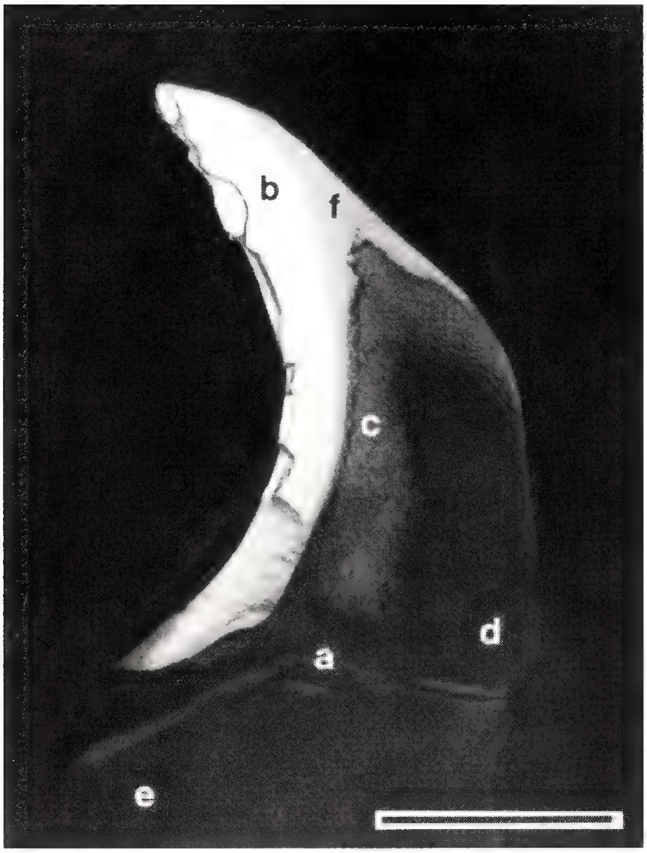
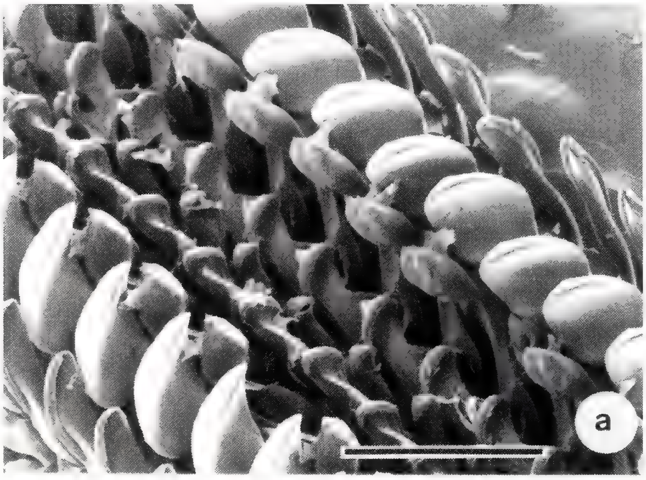


Fig. 1. Backscattered electron micrograph showing a longitudinal section through a major lateral tooth of the type species *Acanthopleura spinosa* during early calcium deposition in the core. Architecturally discrete compartments are visible, corresponding to different biomineralization products. a, the junction zone; b, the magnetite region; c, the anterior core region; d, the central/posterior core region; e, the tooth base and; f, the lepidocrocite region. Scale bar = 100 μm

RESULTS

Light Microscopy

Examination of the radulae of *Acanthopleura* revealed that there was an interspecific, and to a lesser degree, intraspecific variation in the total number of tooth rows, which ranged from a minimum of 46 in *A. rehderi* to a maximum of 108 in *A. brevispinosa*. The radulae contained between five and 14 rows of clear teeth, followed by two to 11 rows of yellow teeth, one to four rows of orange teeth and 30 to 86 rows of black-capped teeth. In the majority of species, the major lateral teeth consisted of a single discoid cusp (Fig. 2a). The teeth of *A. loochooana* were also essentially discoid, but had a small but distinct distal indentation. In contrast, those of *A. rehderi* possessed four short rounded denticles, giving them the appearance of scalloped discs (Fig. 2b). Within the genus *Acanthopleura*, the yellow colouration observed in the early teeth was primarily associated with the junction zone and base of the tooth, while the orange coloured material was found along the posterior cutting surface of the cusps and in the anterior central tab. This orange colour was seen to persist as a thin band for several rows after the initial deposition of the black (magnetite) material in the posterior region. In all but one species, the black magnetite cap covered the entire posterior surface and extended just over the tip onto the anterior surface, forming a tab in the central anterior of the tooth (Fig. 3a). The single exception was *A. rehderi*, in which the magnetite region was restricted to a narrow band at the periphery of the tooth on both the anterior and posterior surfaces and did not form a tab on the anterior surface (Fig. 3b). In all species except *A. rehderi*, a broad reddish/brown band of lepidocrocite was observed on the anterior cusp surface below the magnetite tip, which persisted for the remainder of the radula. The tooth core, as observed



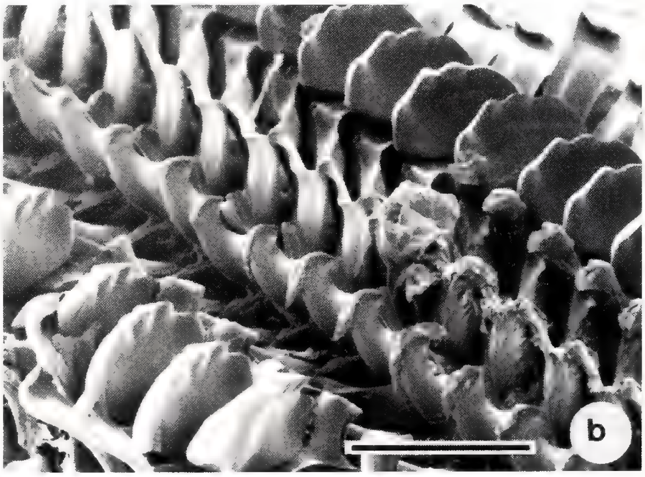


Fig. 2. Secondary electron micrographs of radulae of (a) *Acanthopleura spinosa* showing the discoid shaped, major lateral teeth typical of the genus, and (b) *A. rehderi* illustrating the four denticles present on the cusp. Scale bar = 500 μm (a) and 250 μm (b).

through the anterior surface, changed in colour from a translucent orange to an opaque white or creamy yellow subsequent to the onset of lepidocrocite deposition, although the exact tooth row where this occurred varied with each species,

In comparison, the radula of *Onithochiton quercinus* had an average of 64 tooth rows, and possessed a discoid major lateral tooth with a small medial secondary denticle, giving it a shape similar to a boxing glove. The yellow colouration of the early teeth was distributed as for *Acanthopleura*, while the orange coloured material was limited to the posterior cutting surface of the cusps. The black magnetite covered the posterior surface, stopping just above the proximal junction of the cusp with its base and extending over the margin onto the anterior surface with no indication of a distal tab. No evidence was seen of a lepidocrocite region in the mature teeth, however the core of the cusp could be seen to change from translucent orange to opaque white by the twelfth black tooth. *Ischnochiton australis* had an average of 123 rows of bicuspid teeth, while *Plaxiphora albida* had 68 rows of tricuspid teeth. No lepidocrocite region was present in either species, and the magnetite layer covered the entire posterior surface and extended over the anterior surface, leaving only a small window in the centre, adjacent to the junction zone, through which the core could be seen. The core was observed to change in opacity in the thirteenth black tooth in *P. albida* but not until the thirty-third black tooth in *I. australis*.

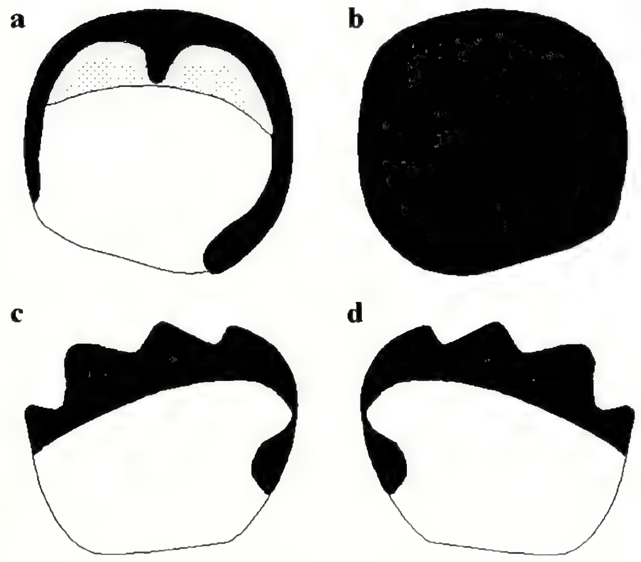


Fig. 3. Diagrammatic representations of a major lateral tooth of *Acanthopleura spinosa* (a and b) and *A. rehderi* (c and d), showing magnetite distribution on the anterior and posterior sides of the tooth respectively.

Scanning electron microscopy and energy dispersive spectroscopy

EDS analyses of the radulae of *Acanthopleura spinosa*, the type species of *Acanthopleura*, together with those of *Ischnochiton australis, Plaxiphora albida*, and *Onithochiton quercinus* revealed that there were substantial differences in the relative percentages of the major elements present in some regions of the major lateral tooth. In all cases the junction zone was the first region in which any elements other than carbon, oxygen and chlorine were detected. Sulfur was usually detected in small amounts in the first yellow tooth, followed by appreciable amounts of iron, calcium, phosphorous and magnesium within one or two tooth rows. In this region of the tooth, the percentages of these elements, particularly that of iron, fluctuated along the radula. However, they exhibited a general trend of an initial rise in the yellow teeth, followed by a fall in the early orange teeth and then a rise to a relatively stable level for the remainder of the radula. The final amounts of each element varied with each species examined, but iron was always the dominant element reaching 35% in *P. albida,* and around 20% in each of the other three species. Phosphorous and magnesium levels were approximately 10% and 2% respectively in all radulae, while calcium ranged from 2% in *P. albida* to 7% in *I. australis* (Figs. 4a, 5a, 6a and 7a).

The next region in which elements were detected was the posterior cutting surface of the tooth. Here iron, accompanied by low levels of phosphorus and calcium together with traces of magnesium and sulfur, was initially found in the tooth row corresponding to the first orange tooth seen at the LM level. In all radulae, the percentage of iron rose rapidly to 60% by the tenth black capped tooth and stabilised within the next 5 rows at approximately 62% for *Acanthopleura spinosa* and *Ischnochiton australis* (Figs. 4b and 5b) and 66% for *Onithochiton quercinus* and *Plaxiphora albida* (Figs. 6b and 7b). These values are comparable to the 66% iron measured in the magnetite standard.

In the early black-capped teeth, the anterior edge of the magnetite region appeared more diffuse than the remainder, with low levels of iron being detected well into the core region of the tooth. In *Plaxiphora albida, Ischnochiton australis* and *Onithochiton quercinus* this condition persisted until the iron levels stabilised. However, in *Acanthopleura spinosa* the early indication of a boundary between the core and magnetite region was observed in the tenth black-capped tooth, at which stage the beginnings of three different regions were apparent in the secondary electron image. The interfaces between these regions became more discrete as the radula matured, with each appearing as a different shade of grey. In the region immediately anterior to the magnetite, iron levels stabilised at

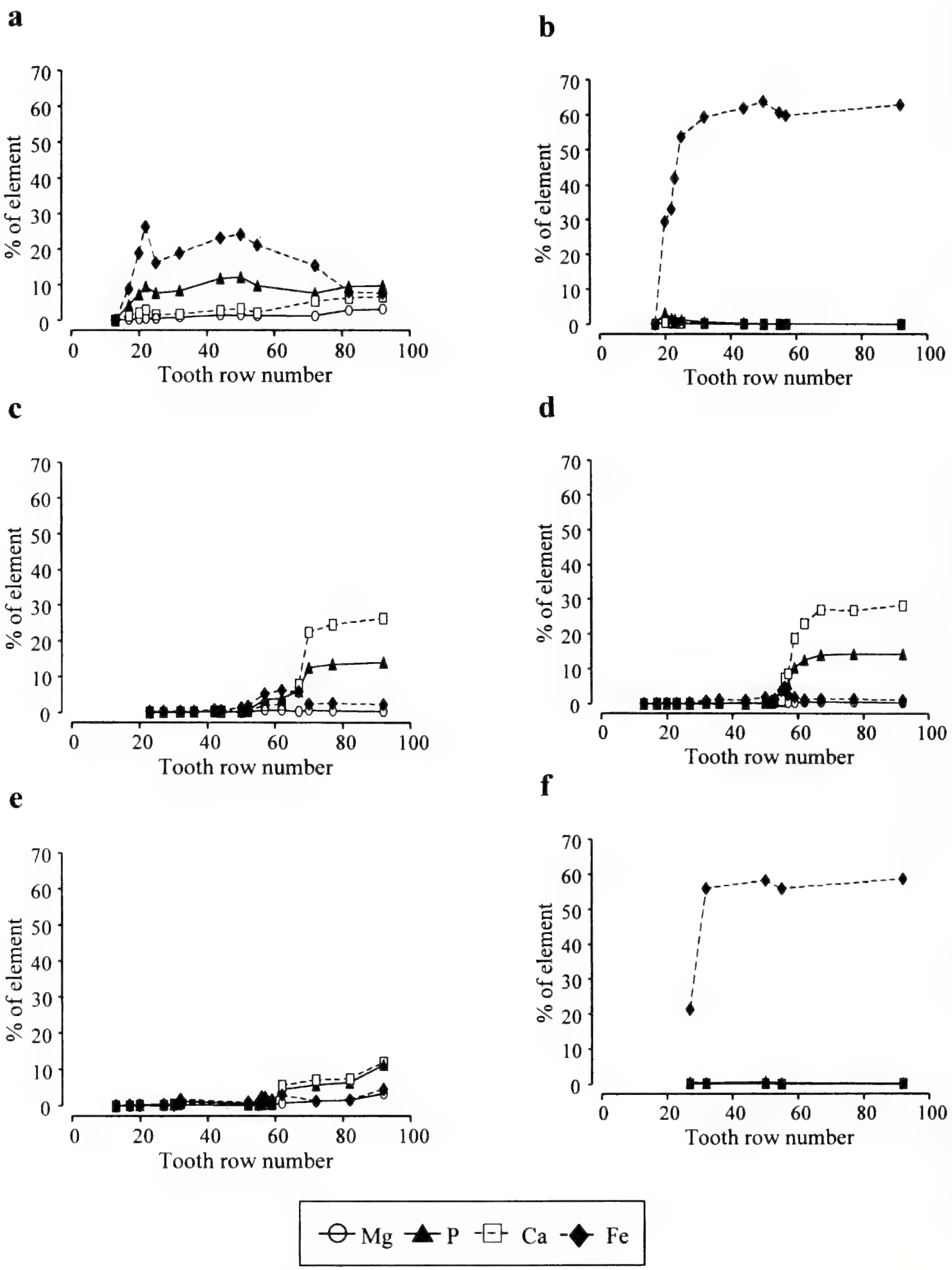


Fig. 4. Quantitative analyses of the major lateral teeth along the length of the radula in *Acanthopleura spinosa*. The main elements present are expressed as a percentage in a, the junction zone; b, the magnetite region; c, the anterior core region; d, the central/ posterior core region; e, the tooth base; and f, the lepidocrocite region.

56% (Fig. 4f), consistently lower than those in the magnetite region and comparable to the 54% measured in the lepidocrocite standard.

In all species it was observed that, due to the polishing procedures, harder regions of the tooth present a smoother, more cohesive appearance under the SEM than softer regions, which also tended to be slightly hollowed out. In the tooth core it was clear from the secondary electron image that mineral deposition was not homogeneous, with certain regions suggesting a harder surface. This harder region commenced in the central posterior region of the core and, over the next few rows, progressed towards the tip and junction zone along the interface with the iron mineralized region. It then spread in an anterior direction with the most anterior region adjacent to the junction zone being the last to infill. Back scattered electron images and X-ray maps confirmed that this feature was indeed associated with the progression of elemental deposition. EDS analysis of the core region indicated that trace amounts of iron, phosphorus, calcium, and sulfur were present in the first orange tooth, and in all radulae iron was initially the dominant element. Levels of the major elements first began to rise in the anterior core region, one or two rows prior to their rise in the central/posterior region. However, in the latter region, levels of the elements rose rapidly and stabilized quickly coinciding with the change in core opacity observed at the LM level. In contrast, in the anterior core region there was a more gradual increase in elements and the final levels were generally lower than those in the central posterior region (cf. Figs. 4c and d, 5c and d, 6c and d and 7c and d). Although there was initially a common pattern of elemental deposition in the core of the tooth, wide inter-generic variation was observed with regard to the stable percentages of the major elements present. For ease of comparison the stable relative percentages of the four major elements present in each of the four genera have been listed in Table 2. In summary, *Acanthopleura spinosa* and *Onithochiton quercinus* exhibited similar elemental ratios with calcium as the dominant element, being double the percentage of phosphorous, while iron and magnesium were present only in low amounts. In contrast, in *Ischnochiton australis* calcium and phosphorus were in equal proportions, magnesium was half their percentage, and iron again was low. Finally, in *Plaxiphora albida* iron was the dominant element, being more than double the amount of phosphorous and approximately four times that of calcium, with only small amounts of magnesium present.

While small amounts of sulfur were found in the bases of the early yellow teeth, appreciable levels of other elements were not detected until after they were found in all other regions of the tooth. The major elements present were again calcium, phosphorus, iron, and magnesium, which attained a maximum of approximately 10, 10, 3 and 3% respectively in *Acanthopleura spinosa* and *Ischnochiton australis* (Figs. 4e, and 5e). *Onithochiton quercinus* differed slightly in that no iron was detected, though the other elemental percentages were the same (Fig. 6e). However, iron was the dominant element at 27% in the base of *Plaxiphora albida*, with phosphorus, calcium and magnesium at 6, 5 and 1% respectively (Fig. 7e).

Within the genus *Acanthopleura* there was an interspecific variation in the tooth row number at which certain stages of biomineralization commenced that was related in most instances to the total number of tooth rows contained in the radula. Thus, in those species with more rows of teeth, the presence of elements other than carbon, oxygen and chlorine was generally not detected until a later tooth row number in all regions examined. As such, the onset of iron deposition in the magnetite region ranged across the genus from row ten in *A. curtisiana*, (radula = 54 rows), to row 23 in *A. brevispinosa*, (radula = 108 rows). Expressed as a percentage of the total number of rows in the radula, the range extended from 16 to 26%. The single exception was *A. rehderi*, where iron deposition did not commence until a third of the way along the radula (35%). Initially, one radula from each additional *Acanthopleura* species was analysed for elemental composition and the results compared to those obtained for *A. spinosa*. If any inconsistencies were found, a further two or three radulae were examined to confirm that the differences were indeed species

Table 2. Major elements found in the core regions of the teeth of four genera from the suborder Chitonina, *Acanthopleura, Ischnochiton, Onithochiton,* and *Plaxiphora*. Data are expressed as a percentage of the total composition. Oxygen, carbon and chlorine have not been included.

Tooth region	Element	*A. spinosa*	*I. australis*	*O. quercinus*	*P. albida*
Central-posterior core	Iron	1	6	0.2	27
	Phosphorous	14	14	15	11
	Calcium	27	17	31	6
	Magnesium	0.5	2	0.3	2
Anterior core	Iron	2	4	0.2	17
	Phosphorous	13	12	15	14
	Calcium	24	12	30	7
	Magnesium	0.4	5	0.3	3

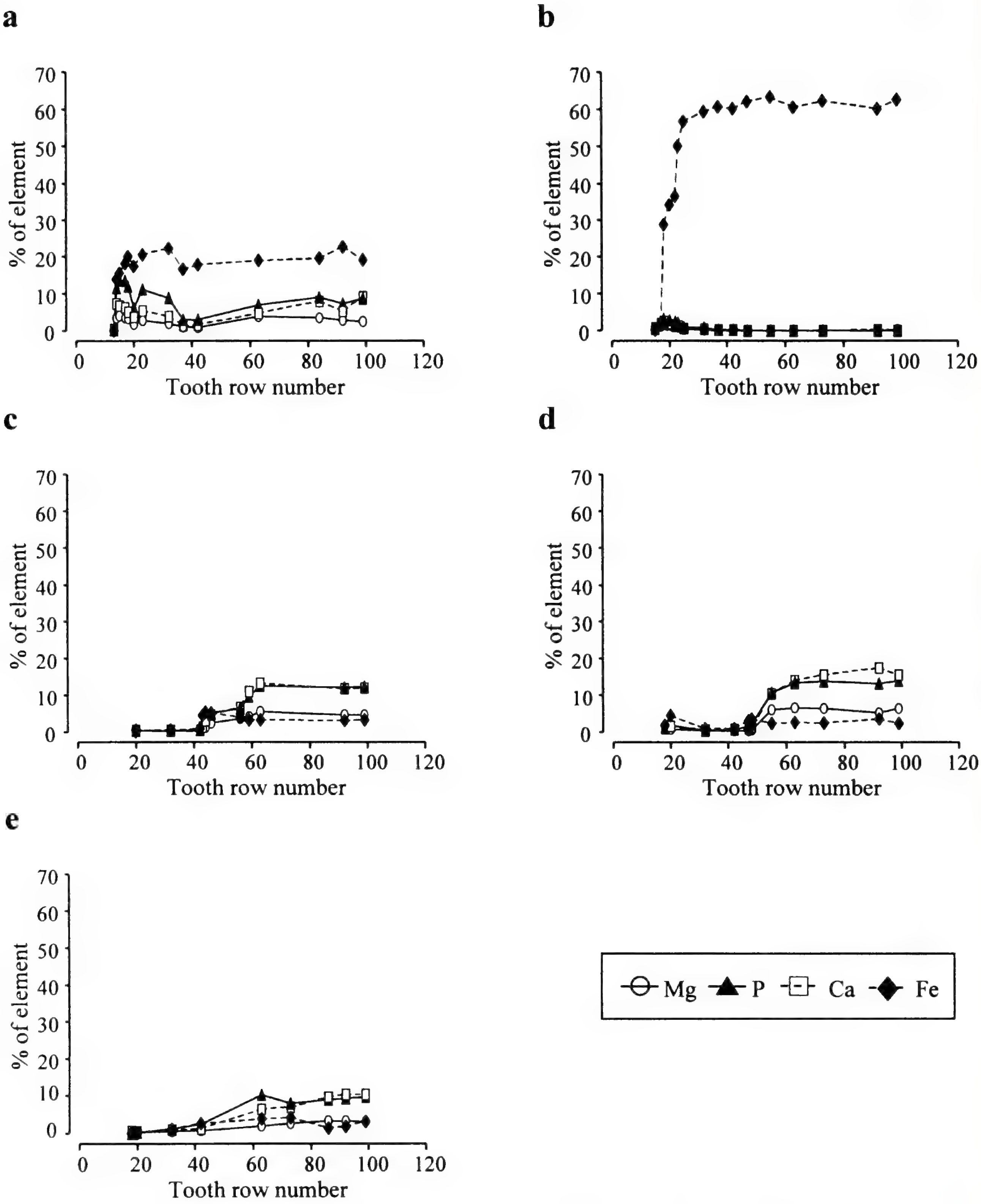


Fig. 5. Quantitative analyses of the major lateral teeth along the length of the radula in *Ischnochiton australis*. Data and regions are as given in Figs. 4a, b, c, d, and e.

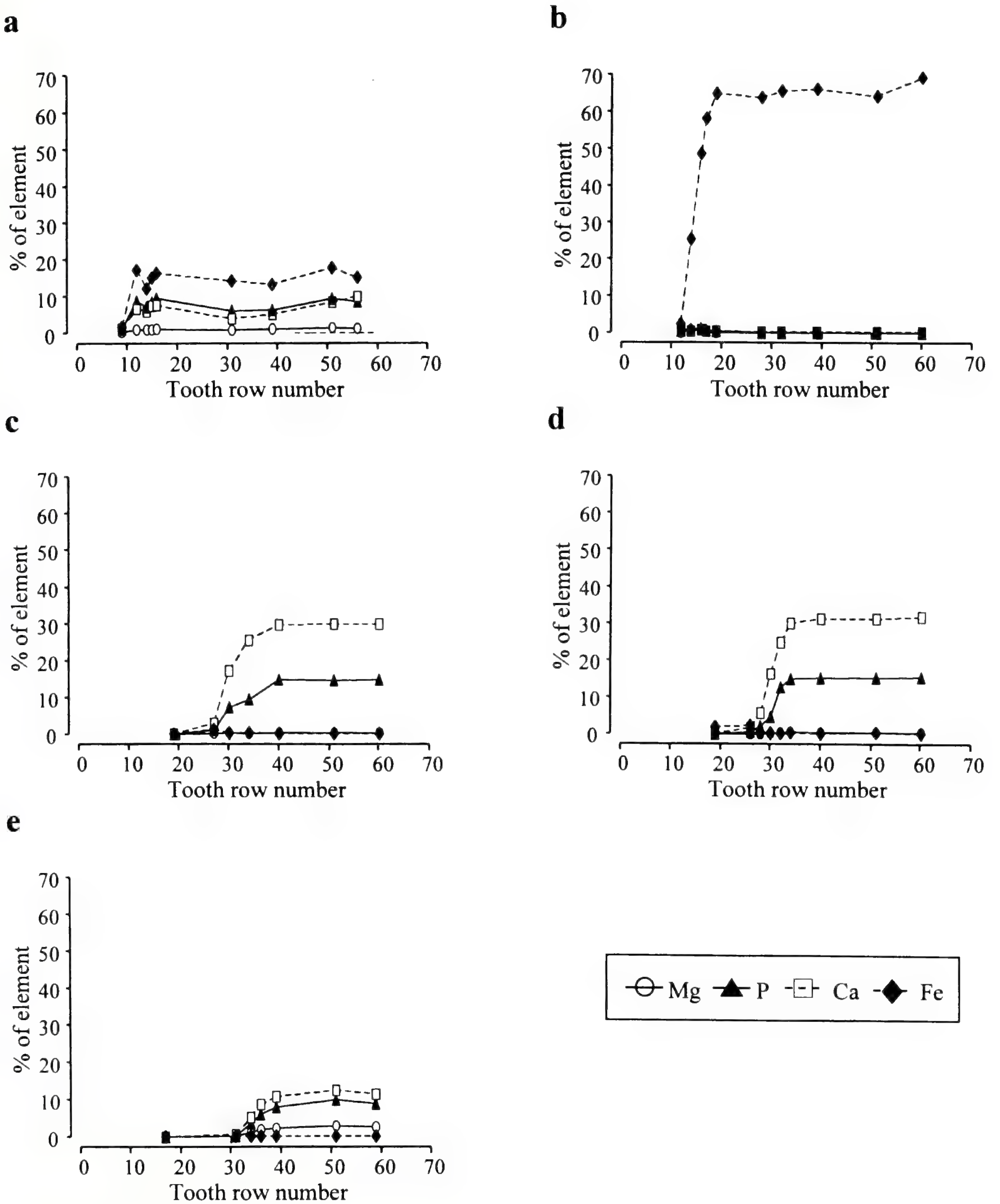


Fig. 6. Quantitative analyses of the major lateral teeth along the length of the radula in *Onithochiton quercinus*. Data and regions are as given in Figs. 4a, b, c, d, and e.

specific. As such, the results reported here are from the species that deviated in some way from those of the type species. In all species the percentage of iron in the magnetite region reached a plateau at a level close to that of the magnetite standard with a range between 62 and 68%. The early differentiation of the posterior iron-mineralising region into magnetite and lepidocrocite was not always obvious in all radulae, but in general it occurred between the tenth and twentieth black capped teeth. Again, the only exception to this was *A. rehderi* whose major lateral teeth did not contain a lepidocrocite region at any stage of development. The pattern of elemental deposition in the core was generally the same as for *A. spinosa*, with calcium and phosphorous initially occurring in the anterior region and increasing gradually over the next 9 to 20 rows, while in the central/posterior region their appearance was delayed by one or two rows but then peaked rapidly over the next two to five rows. The percentage of iron in the core of the mature teeth was relatively low in most species, ranging from 0 to 1.7% in the central posterior core and from 0 to 2% in the anterior core region. However, in *A. curtisiana, A. miles, A. araucariana* and *A. loochooana* it was substantially higher, ranging from 4 to 7% in the central/posterior core and from 4.3 to 14% in the anterior core region.

Analysis of resin-only control blocks revealed that the major elements present were carbon and chlorine, attributable to the resin, with small amounts of aluminium, presumably from the mounting ring, and traces of silicon from the abrasive.

DISCUSSION

Within the suborder Chitonina the major lateral tooth cusps exhibit a wide degree of variation, both in terms of form, possessing between one and four denticles, and biomineralization, with at least three distinct strategies being identified. Thus, between the genera the major differences encountered relate to the presence or absence of lepidocrocite and the different combination of core elements, which in turn produce a range of mineral components. Furthermore, while the process of magnetite deposition is remarkably consistent across all of the genera examined, there is considerable variation in the distribution of this mineral within the tooth, predominantly with regard to the extent of its coverage of the anterior tooth surface, but also in the case of *Acanthopleura rehderi* with its restricted posterior distribution.

Of the three biomineralization strategies described in this paper, two have been documented previously (Lowenstam and Weiner, 1989; Macey and Brooker, 1996). However, that presented here for *Ischnochiton australis* clearly differs from those already described in the literature in that there are almost equal quantities of calcium and phosphorous, in addition to substantial amounts of magnesium, in the core (cf. Figs. 4d, 5d and 7d). Indeed, the elemental ratio in this region is comparable to that found in the mineral whitlockite $(Ca_{18}H_2(Mg,Fe)^{2}{}_{2}+(PO_4)_{14})$. The reason for such high levels of magnesium in the core can only be surmised at this stage but this element is known to inhibit the conversion of amorphous calcium phosphate (ACP) to crystalline hydroxyapatite (Lowenstam and Weiner, 1989).

Generally, within the genus *Acanthopleura*, the shape of the major lateral tooth shows limited deviation from the concave disc of the type species. Likewise, biomineralization is similar in most species and is consistent with that previously described for *A. hirtosa* (Kim *et al.*, 1989; Evans *et al.*, 1992, Lee *et al.*, 1998). The most remarkable exception to the type pattern occurs in *A. rehderi*, which is the sole member of *Acanthopleura* to have major lateral teeth possessing four denticles. In addition, magnetite distribution in these teeth is conspicuously different in that it is only found in a band along the anterior and posterior margin of the tooth and neither forms a tab on the anterior surface, nor extends to the junction zone on the posterior surface. It is also apparent from secondary electron images and EDS analysis that no lepidocrocite region separates the magnetite from the core. Finally, iron mineralization does not commence in *A. rehderi* until much further along the radula, 35% compared to 16 to 26% in the other *Acanthopleura* species, indicating that this species has a far greater proportion of unmineralized teeth than all other members of the genus. In many of these regards *A. rehderi* bears a closer resemblance to *Onithochiton quercinus*, whose major lateral teeth have a small medial secondary denticle, do not possess a lepidocrocite region or an anterior magnetite tab and whose magnetite cap, though more extensive than that of *A. rehderi*, does not extend completely to the junction of the tooth with its base. Although the major lateral cusps of *A. loochooana* also display a slight variation from the typical disc of the genus by possessing a small distal indentation, they do not exhibit any substantial deviation in terms of their distribution of iron minerals in these teeth.

In previous studies, the cores of the major lateral teeth of *Acanthopleura echinata, A. gemmata, A. haddoni* and *A. hirtosa* have been shown to contain one of a variety of forms of the mineral apatite (Lowenstam, 1967; Lowenstam and Weiner, 1985; Evans *et al.*, 1992). Microanalysis of core fractions from *A. echinata* indicate that it is composed of approximately 32% calcium and 16% phosphorus (Lowenstam, 1967), with no measurable amounts of iron, which is consistent with the data obtained for the majority of *Acanthopleura* species in this study. Although the stable percentages of calcium and

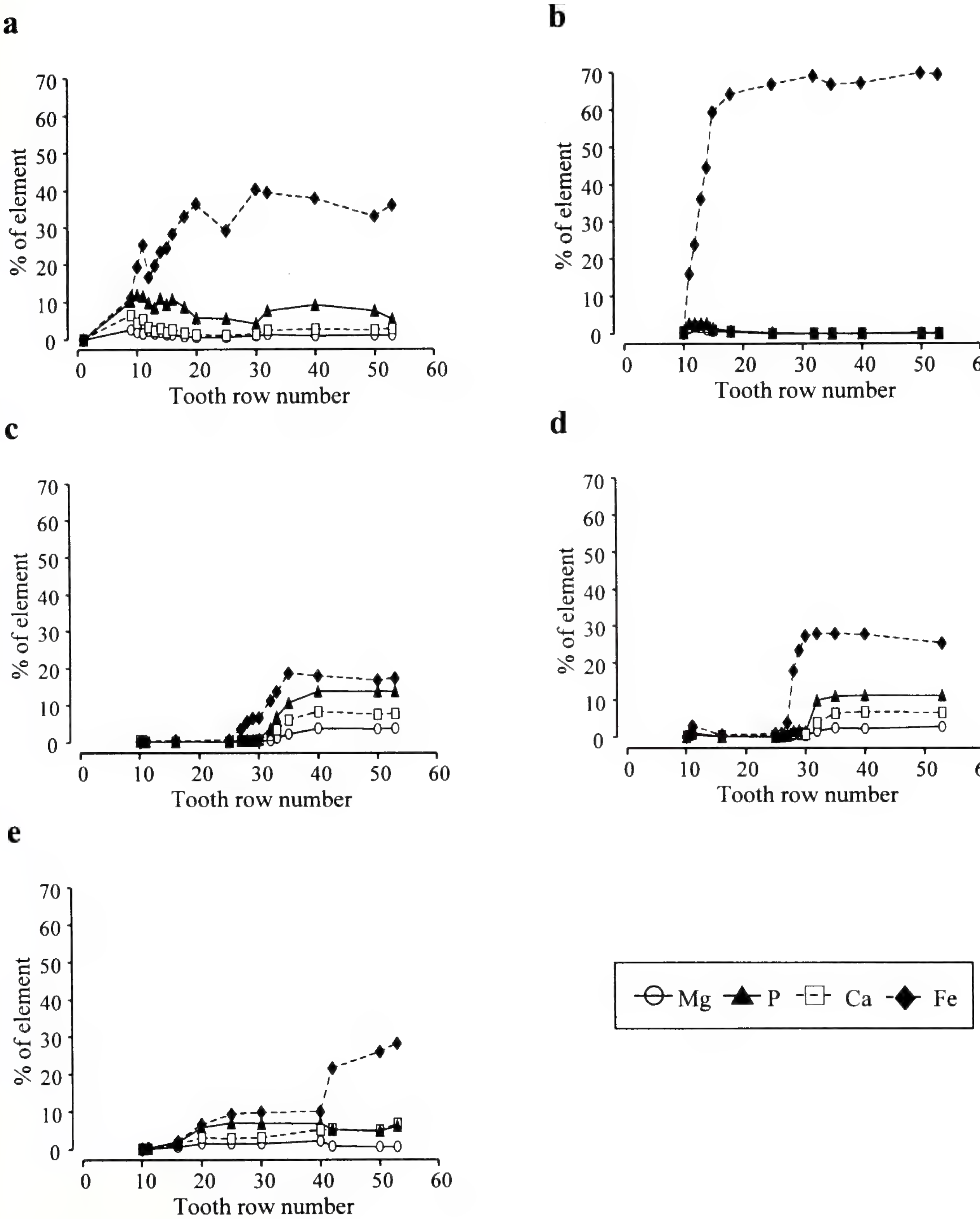


Fig. 7. Quantitative analyses of the major lateral teeth along the length of the radula in *Plaxiphora albida*. Data and regions are as given in Figs. 4a, b, c, d, and e.

phosphorous in the mature teeth show some interspecific variation, in most instances calcium levels are approximately double that of phosphorous, while iron is less than 2%. However, in four species, *A. curtisiana, A. miles, A. araucariana* and *A. loochooana*, the level of iron in the core is substantially higher, ranging from 4 to 14% in different core regions. Prior to Ferreira's (1986) revision of *Acanthopleura*, the first three of these species comprised the separate genus *Squamopleura*, into which they were assigned mainly on the basis of similarities of their girdle scales. Ferreira considered the various girdle elements of *Acanthopleura* species to be analogous characters, whether they are spines, spinelets or scales, since they are all implanted in the girdle in a similar manner (Ferreira, 1986). However, the similar elemental composition of the core of these three species, together with their variance to other members of the genus, corroborates the hypothesis that the girdle distinctions previously noted are due to homologous resemblance and suggests that there could well be a basis to their separation from *Acanthopleura*. The fourth species, *A. loochooana*, shares more than just its unusual core composition with the three *Squamopleura* species since they all have underdeveloped insertion teeth and limited pectination of the posterior valve. This is a character used extensively in chiton taxonomy, but one that is also common to some other members of *Acanthopleura*.

Within the Polyplacophora the shape of the major lateral teeth has long been considered of taxonomic importance and is now frequently included in descriptions of taxa at all levels (Ferreira, 1986; Bullock, 1988; Kaas and Van Belle, 1985-1994). On the evidence presented in this paper it is clear that a relationship exists between tooth shape and elemental ratios, which indicates that the biomineralization strategy employed could be used as a reliable taxonomic character. Within the genus *Acanthopleura*, biomineralization is remarkably consistent for 13 of the 18 nominal species examined. However, the evidence suggests there could be a case for the resurrection of the genus *Squamopleura*, albeit the many similarities that exist between the members of this suppressed genus and *A. loochooana* suggests a strong link between the two genera. Moreover, the radically different radula teeth of *A. rehderi* indicate that its inclusion in the genus is also debatable, especially considering their closer affinity with those of *Onithochiton quercinus*. However, despite the differences encountered, the biomineralization strategies employed by all *Acanthopleura* species still bear a greater resemblance to each other than they do to those of either *Ischnochiton australis* or *Plaxiphora albida*. This study has considered just one aspect of generic differentiation and species relatedness and a decision regarding the status of the genus *Acanthopleura* should be deferred until as many characters as possible have been analysed and collated.

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Shell and ligament microstructure of selected Silurian and Recent palaeotaxodonts (Mollusca: Bivalvia)

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Abstract: Silurian *Praenucula faba* Liljedahl, 1994, had a nacroprismatic shell and a submarginal, simple, amphidetic ligament with a posterior, lamellar/fibrous component and an anterior, lamellar component. Praenuculids are suitable ancestors for both nacroprismatic nuculids such as *Nuculoidea pinguis* (Lindström, 1880), and nacroprismatic "ctenodontids" such as *Tancrediopsis gotlandica* (Soot-Ryen, 1964). Nuculids evolved by shortening and submerging the posterior part of their ancestral simple ligament to make an internal resilium, whereas solemyoids, including "ctenodontids", elevated the posterior part of their ancestral simple ligament to make a parivincular ligament. Judging from Silurian *Tancrediopsis*, "ctenodontids" were morphologically, microstructurally, and ligamentally well suited for ancestry to the Solemyoidea. Within the Silurian-Recent family Nuculidae, the Nuculominae Maxwell, 1988 retained largely nacreous shells without denticular composite prisms; the Nuculinae Gray, 1824, retained largely nacreous shells but evolved denticular composite prisms; and the Palaeonuculinae *subfam. nov.* evolved largely porcelaneous shells without denticular composite prisms. Palaeonuculines differ from pristiglomid nuculoideans in retaining traces of ancestral laminar structure in the form of matted structure or early juvenile nacre.

The family Cardiolariidae Cope, 1997 is characterized primarily by anterior palaeotaxodont or pseudotaxodont hinge teeth that are abruptly enlarged relative to posterior palaeotaxodont teeth, and by the plesiomorphic absence of a resilium. Although the Silurian cardiolariid *Ekstadia tricarinata* Soot-Ryen, 1964 is porcelaneous, earlier cardiolariids may have been nacreous.

The presence of at least minor amounts of large tablet, imbricated nacre in Early Cambrian *Anabarella* Vostokova, 1962, *Watsonella* Grabau, 1900, *Pojetaia runnegari* Jell, 1980, and *Fordilla troyensis* Barrande, 1881 indicates that this feature is plesiomorphic for the Bivalvia rather than synapomorphic for "fordilloids". As a paraphyletic grade, "fordilloids" document the evolutionary transition in shell and ligament microstructure from laterally compressed monoplacophorans to crown group bivalves.

Key Words: Bivalvia, Palaeotaxodonta, ligaments, shell microstructure, evolution, Palaeonuculinae

The Palaeotaxodonta Korobkov, 1954, is an ancient subclass of medium-size to minute, equivalve, marine bivalves characterized by test-cell larvae, a deeply cleft foot with papillate edges, palp proboscides, distinctive stomach anatomy, and the lack of a crystalline style (Waller, 1998). Palaeotaxodonts are also characterized by particular patterns of pedal and adductor musculature, and variably developed or secondarily reduced palaeotaxodont hinge teeth (Carter *et al.*, 2000). Shell microstructure in the subclass Palaeotaxodonta has long been recognized as convergent on other bivalves, but it is nevertheless important for defining palaeotaxodont families and subfamilies (Douvillé, 1913; Schenck, 1934; Taylor *et al.*, 1969; Maxwell, 1988; Carter, 1990). The shell microstructures in this subclass are richly varied, with outer layers ranging from homogeneous to fibrous prismatic, simple prismatic, spherulitic prismatic, dissected crossed prismatic, and denticular composite prismatic, and middle and inner layers ranging from nacreous to homogeneous, matted, crossed acicular, simple crossed lamellar, and complex crossed lamellar (Bøggild, 1930; Taylor *et al.*, 1969; Carter, 1990; among others). The superfamilies Nuculoidea Gray, 1824, Nuculanoidea Adams and Adams, 1858, and Solemyoidea Gray, 1840 each include nacreous and non-nacreous taxa, with nacre representing the ancestral middle and inner layer microstructure (Douvillé, 1913; Taylor, 1973; Carter, 1990). Palaeotaxodont ligaments are similarly diverse, with an ancestral dorsal, simple ligament supplemented evolutionarily by a resilium in certain nuculoids and nuculanoids, or modified into a parivincular ligament in solemyoids. The resilia may be fully mineralized or only laterally mineralized, and their mineralization may be fibrous and/or granular (Waller, 1990; Carter, 1990).

Very little is known about early palaeotaxodont shell and ligament microstructure. Published accounts of pre-Devonian palaeotaxodont microstructure are limited to observations of relict nacre in Ordovician *Palaeoconcha* sp. (Mutvei, 1983), and *Deceptrix levata* (Hall, 1847) (Carter *et al.*, 1990a:303). Microstructural relicts have also been described for Cambrian *Pojetaia* Jell, 1980, and *Fordilla* Barrande, 1881 (Runnegar, 1983, 1985; Runnegar and Bentley, 1983; Runnegar and Pojeta, 1985, 1992; Geyer

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and Streng, 1998), but these "fordilloids" remain controversial with regard to their relationship with crown group bivalves (see discussion, below).

The present paper describes the shell and ligament microstructure of four Upper Silurian palaeotaxodonts from the Mulde Formation of Gotland, Sweden, and three Recent palaeotaxodonts. These are the first descriptions of shell and ligament microstructure for a cardiolariid, praenuculid, "ctenodontid," and pristiglomid, and for a Recent member of the nuculid subfamily Palaeonuculinae *nov*.

The taxonomic arrangement of this paper follows the phylogenetic classification by Carter *et al.* (in press), but with inclusion of the family Pristiglomidae Sanders and Allen, 1973 in the superfamily Nuculoidea, and with subdivision of the Nuculidae into three subfamilies.

MATERIALS AND METHODS

Specimens of Recent *Pristigloma nitens* (Jeffreys, 1876) were provided by Dr. John A. Allen of the University Marine Biological Station, Millport, Isle of Cumbrae, Scotland. Topotype specimens of Recent *Condylonucula maya* Moore, 1977, were donated by the late Dr. Donald R. Moore. The loan of Silurian palaeotaxodonts from Gotland was arranged by Ingela Chef-Holmberg of the Swedish Museum of Natural History, Stockholm. Most of the Silurian Gotland specimens came from the Wenlockian, Upper Silurian Mulde Formation near Djupvik. Some of the Silurian specimens lacked detailed locality information, but their color and preservation suggest this same provenance. The geologic and stratigraphic setting of the Mulde Formation has been described by Kershaw (1993) and Munnecke *et al.* (1999). The Silurian fossils are now deposited at the Swedish Museum of Natural History, Box 50007, S-104 05, Stockholm, Sweden (RMMo). The Recent nuculoideans are deposited at the Yale University Peabody Museum of Natural History (YPM).

The methods of microstructure analysis follow Carter and Ambrose (1989). The terminology of shell and ligament microstructure is based on Waller (1990), Carter (1990), and Carter *et al.* (1990b). Abbreviations in the text and figures are:

ALL: anterior lamellar ligament
CA: crossed acicular
CCL: complex crossed lamellar
CL: (simple) crossed lamellar
FCCL: fine complex crossed lamellar
FL: fibrous ligament
Fo: fossette
HOM: homogeneous
ICCL: irregular complex crossed lamellar
N: nacreous
P: prismatic
PFL: posterior fibrous ligament
RMMo: Swedish Museum of Natural History, Stockholm
UNC: University of North Carolina at Chapel Hill
YPM: Yale Peabody Museum

MICROSTRUCTURAL PRESERVATION

Bivalves from the Upper Silurian Mulde Formation are preserved in a manner similar to those described by Carter and Tevesz (1978a, 1978b) and Carter (1990) from the Middle Devonian Hamilton Group near Morrisville, New York. Relict shell and ligament microstructures are visible in acetate peels of diagenetic replacement calcite, even though fracture surfaces and x-ray diffraction give no indication of preserved aragonite. This preservation differs from that described by Sandberg and Hudson (1983) for Jurassic calcite-replaced bivalves, where some original aragonite is still present. Microstructural relicts in the Silurian shells probably reflect differential etching rates induced by organic matrices. Darker colored specimens are commonly better preserved than lighter colored ones, suggesting that reducing conditions have favored the retention of this matrix. All presently examined Silurian bivalves were originally aragonitic, based on their microstructures and uniform alteration to calcite.

Studying relict shell and ligament microstructure commonly requires multiple sections through the same shell, and in some instances the examination of several shells to obtain adequate information for every shell layer. The excellent relict preservation of some of the present Silurian shells can be illustrated by comparing acetate peels of Carboniferous, nacroprismatic nuculids and polidevciids with original aragonite (Fig. 1.1, 1.2), with acetate peels of Silurian, nacroprismatic *Praenucula* and *Tancrediopsis* with recrystallized shells (Fig. 1.3, 1.4). Finely prismatic, crossed acicular, and fine complex crossed lamellar structures in a modern malletiid (Fig. 2.1-2.3) can similarly be compared with the same microstructures in Silurian *Ekstadia* (Figs. 2.4, 2.5).

The present descriptions of relict ligaments are based on dorsoventral, serial sections through united valves, supplemented by Liljedahl's (1994) excellent illustrations of prepared hinges and ligament insertion areas. Mineralized ligament sublayers are generally well preserved in the Mulde bivalves (Figs. 1.5, 1.6). The former presence of lamellar ligament can be inferred from localized concentrations of framboidal pyrite. However, caution must be exercised in doing so, because pyrite can also be concentrated in other enclosed or semi-enclosed spaces influenced by the reducing chemistry of tissue

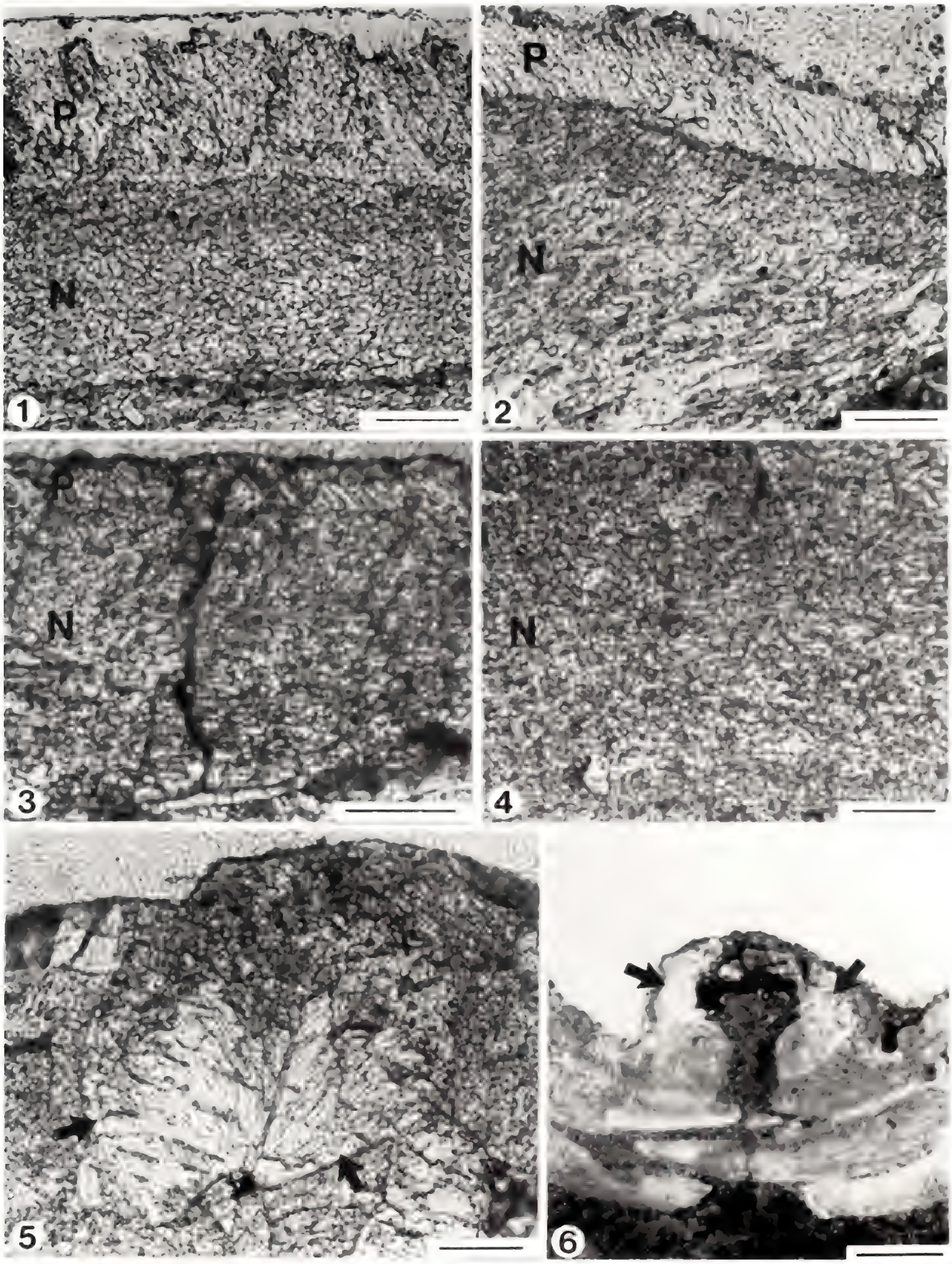

Fig. 1. Acetate peels of dorsoventral sections through Silurian and Carboniferous palaeotaxodonts, showing prismatic outer layers (P), nacre (N), and fibrous ligament (at arrows); shell exterior is up in all figures; the ventral shell margin is toward the right in 1.1-1.3; bar scales = 50 µm in 1.1-1.5, 500 µm in 1.6. 1.1, radial, ventral section through the prismatic outer and nacreous middle layers of Upper Carboniferous *Nuculopsis girtyi* Schenck, 1934, Magoffin Member of Breathitt Formation, Daniel Boone Parkway near Hazard, Kentucky, UNC 7357; original shell aragonite is preserved. 1.2, radial, ventral section through the prismatic outer and nacreous middle shell layers of Upper Carboniferous *Phestia bellistriata* (Stevens, 1858), Kendrick Shale Member of Breathitt Formation, Floyd County, Kentucky, UNC 13649; original aragonite is preserved. 1.3, radial, ventral section through Upper Silurian *Praenucula faba* Liljedahl, 1994, Mulde Formation, Djupvik, Gotland, Sweden, RMMo 15908, showing relict prismatic outer and nacreous middle shell layers. 1.4, relict nacreous laminae in the umbonal inner shell layer of Upper Silurian *Tancrediopsis gotlandica* (Soot-Ryen, 1964), Mulde Formation, Djupvik, Gotland, Sweden, RMMo 15768. 1.5, relict ligament fibers in the submarginal, simple ligament of Upper Silurian *Ekstadia tricarinata* Soot-Ryen, 1964, Mulde Formation, Djupvik, Gotland, Sweden, RMMo 15469; the fibrous ligament is flanked by porcelaneous structure, here poorly preserved, and is overlain by a concentration of framboidal pyrite that suggests the former presence of lamellar ligament. 1.6, transverse section through the parivincular ligament and hinge of *T. gotlandica*.

decomposition. Lamellar ligament is presently inferred to have been present only if pyrite is localized in a position compatible with the presence of ligament, *e.g.*, between submarginal fossettes or internal resilifers, and if the pyrite is significantly more concentrated than in adjacent restricted spaces. For example, framboidal pyrite is highly concentrated between the resilifers of *Nuculoidea pinguis* (Lindström, 1880), but not within its adjacent shell interior (Fig. 6.6). On the other hand, the anterior, submarginal fossettes in *Tancrediopsis gotlandica* (Soot-Ryen, 1964) do not provide unequivocal evidence for lamellar ligament because their pyrite is only slightly more concentrated than between the adjacent hinge teeth (Fig. 9.5). Relict lamellar ligament in a dorsal, submarginal fossette cannot be differentiated from overlying relict periostracum. However, dorsal, submarginal fossettes in modern palaeotaxodonts are either non-ligamental, in which case the periostracum, if it spans the valves, generally does not descend deeply within the fossette, or they are ligamental, in which case the fossette is filled primarily by lamellar and perhaps also fibrous ligament, with relatively little periostracum deposited within the fossette.

OBSERVATIONS OF SHELL AND LIGAMENT MICROSTRUCTURE

Subclass Palaeotaxodonta Korobkov, 1954

Carter *et al.* (2000) divided the subclass Palaeotaxodonta into the monophyletic superorders Nuculaniformii Adams and Adams, 1858, and Nuculiformii Gray, 1824. The Nuculiformii shows a basal dichotomy between *Eritropis* Pojeta and Gilbert-Tomlinson, 1977, and the rest of the superorder, followed by a dichotomy between the Cardiolariidae Cope, 1997, and an unnamed clade in which the Tironuculidae Babin, 1982, Praenuculidae McAlester, 1969, and the clade of Nuculoida plus Solemyoida differentiate in that sequence. Within the Solemyoida, *Tancrediopsis* Beushausen, 1895, is basal to the clade of *Ctenodonta* Salter, 1852 plus Solemyoidea Gray, 1840.

Superorder Nuculiformii Gray, 1824
Family Cardiolariidae Cope, 1997

Cope (1997:736) provided the following diagnosis for the Cardiolariidae: "Palaeotaxodonts with separate anterior and posterior dentitions, in which the hinge lies along line of posterior teeth; anterior teeth, which may be enlarged, lie below hinge axis. Ligament external, opisthodetic." External, opisthodetic ligaments and ventrally positioned, anterior hinge teeth are not, however, unique to the Cardiolariidae. These two features also characterize certain praenuculids, such as *Palaeoconcha* Miller, 1889, and *Similodonta* Soot-Ryen, 1964. The cardiolariids *Cardiolaria beirensis* (Sharpe, 1853) and *Praeleda subtilis* Cope, 1999, have anterior hinge teeth that differ from the typical palaeotaxodont pattern in number and/or arrangement, but this is similarly not diagnostic of their family. The cardiolariids *Praeleda costae* (Sharpe, 1853), and *Deceptrix carinata* Fuchs, 1919 have more typical anterior, palaeotaxodont hinge teeth (see Cope, 1997, text-fig. 3). Based on the phylogenetic analysis in Carter *et al.* (2000), a more appropriate diagnosis for the Cardiolariidae is the presence of anterior palaeotaxodont or pseudotaxodont hinge teeth abruptly enlarged relative to posterior palaeotaxodont hinge teeth, *i. e.*, "heterotaxodonty", and the plesiomorphic retention of an opisthodetic, simple ligament without a resilium.

Soot-Ryen (1964:502) placed *Ekstadia* in the family Ctenodontidae, whereas Liljedahl (1994) transferred it to the nuculanoidean family Malletiidae Adams and Adams, 1858, largely on the basis of its pallial sinus. *Ekstadia tricarinata* Soot-Ryen, 1964 resembles *Cardiolaria beirensis* and *Praeleda subtilis* in having a heterotaxodont hinge, an opisthodetic, simple ligament, and no resilium. It also resembles *P. compar* (Barrande, 1881) in having a pallial sinus (Pfab, 1934, pl. 3, fig. 7). On the basis of these similarities, Carter *et al.* (2000) placed *Ekstadia* in the Cardiolariidae.

Except for possible relict nacre in Ordovician *Deceptrix levata* (Hall, 1847) (Carter *et al.*, 1990a:303), cardiolariid shell microstructure has not previously been described.

Ekstadia tricarinata Soot-Ryen, 1964 (Figs. 1.5, 2.4, 2.5, 3, 4)

Liljedahl (1994) reported that *Ekstadia* has an external, opisthodetic ligament. However, the "nymph" that he illustrated for *Ekstadia kellyi* Liljedahl, 1994, (his fig. 34K) is the margin of a fossette for a submarginal, simple ligament. The present observations of *E. tricarinata* are based on ten dorsoventral sections and two anteroventral, commarginal to oblique sections through a pair of valves 8.2 mm in length (RMMo 15469; Fig. 3.7), and five dorsoventral sections and the anterior part of one anteroposterior section through a second pair of valves, also 8.2 mm in length (RMMo 15468).

The ligament is simple and opisthodetic, with a planar to slightly arched, fibrous sublayer inserting into rounded to V-shaped (in cross section), submarginal fossettes (Figs. 1.5, 3.2-3.6, 4.5). The fossettes extend anteriorly only as far as the beaks (Fig. 4.5). The fibrous portion of the ligament is thick in comparison with the hinge, and extends continuously between the valves (Figs. 1.5, 3.2-3.6). Concentrations of framboidal pyrite are compatible with the former presence of lamellar ligament in the dorsal part of

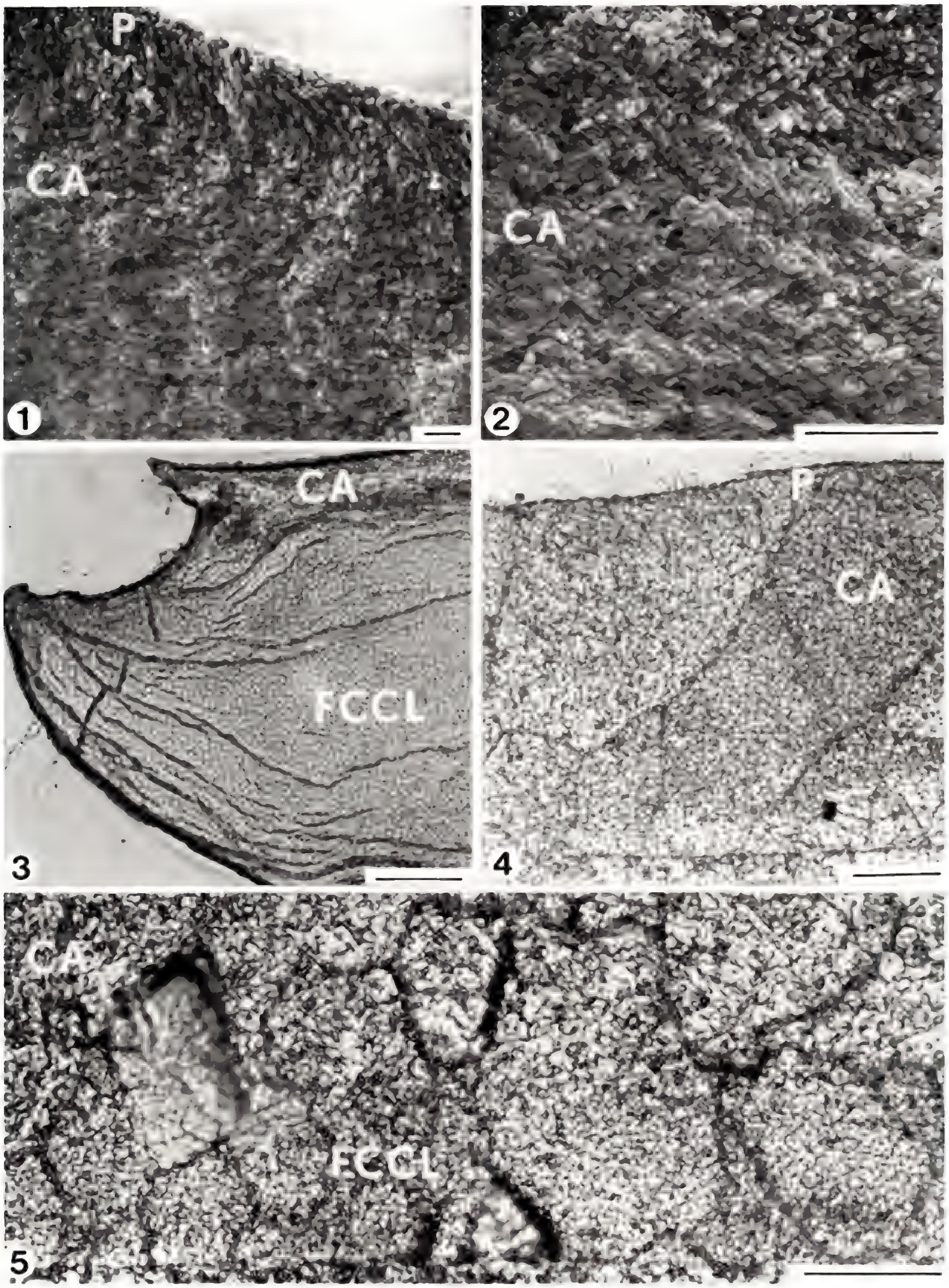

Fig. 2. Shell microstructure of Recent and Silurian malletiids. 2.1-2.3, reclined, prismatic (P), crossed acicular (CA), and fine complex crossed lamellar (FCCL) structures in Recent *Malletia obtusa* Sars, 1872, U.S. Fish Commission Station 2221, Atlantic Ocean. 2.1, SEM of radial fracture through posterior shell margin; shell exterior is up and posterior margin is toward the right; bar scale = 10 µm. 2.2, SEM of commarginal, vertical fracture near ventral shell margin, showing the two predominant dip directions of the crossed acicular, middle shell layer; shell exterior is up; bar scale = 5 µm. 2.3, dorsoventral, vertical acetate peel through the posterior hinge; dorsal exterior of shell is up and hinge dentition is toward the left; the prismatic outer shell layer is not recognizable in this section; bar scale = 50 µm. 2.4, 2.5, relict prismatic (P), crossed acicular (CA) and fine complex crossed lamellar (FCCL) structures in the Upper Silurian malletiid *Ekstadia tricarinata* Soot-Ryen, 1964, RMMo 15469. 2.4, acetate peel of a radial, vertical section near the anteroventral shell margin, showing the prismatic outer and crossed acicular middle shell layers; the shell exterior is up and the anteroventral shell margin is toward the right; bar scale = 50 µm. 2.5, acetate peel of an anteroventral, commarginal (transverse) section showing the boundary between the crossed acicular middle shell layer and the underlying FCCL inner shell layer; note that the dip directions in the CA structure cross diagenetic calcite crystal boundaries; the shell interior is near the bottom of the photograph; bar scale = 50 µm.

the fossette, although the thickness of this sublayer is unknown. A thin lamellar sublayer is hypothesized in Figs. 3.3-3.6. There is no evidence for a resilium.

The shell margins are smooth and thinly tapering. The outer shell layer is relatively thin and inconspicuous, and consists of fine, reclined prisms (Figs. 2.4, 4.4). The middle and inner shell layers are predominantly crossed acicular and fine complex crossed lamellar, respectively (Figs. 2.4, 2.5; 4.1-4.4). They are locally separated by an irregular simple prismatic pallial myostracum (Fig. 4.3). An internal shell blister was observed in one specimen (Fig. 4.1-4.3). The hinge consists primarily of fine complex crossed lamellar and possibly also homogeneous structure.

Family Praenuculidae McAlester, 1969

McAlester (1969) described the Praenuculidae as having an external ligament and no resilifer, thereby correcting Cox's (1959) reference to a resilifer in *Praenucula* Pfab, 1934. McAlester's (1969) placement of praenuculids in the superfamily "Nuculacea" also implied a truncate shell posterior and no pallial sinus. Cope (1997) restricted the Praenuculidae to "gradidentate" taxa, *i.e.*, with hinge teeth gradually increasing in size anteriorly and posteriorly from the subumbonal region. This family includes *Praenucula* Pfab, 1934, *Ledopsis* Beushausen, 1884, *Palaeoconcha* Miller, 1889, *Similodonta* Soot-Ryen, 1964, *Homilodonta* Cope, 1997, *Concavodonta* Babin and Melou, 1972, *Fidera* Pojeta and Gilbert-Tomlinson, 1977, and *Arcodonta* Cope, 1999, among others. According to Waller (1998:17), praenuculids range from Early Ordovician to at least Devonian and possibly Late Permian.

The Praenuculidae are commonly regarded as plesiomorphic members of the superfamily Nuculoidea (McAlester 1969; Pojeta and Gilbert-Tomlinson, 1977; Babin and Gutiérrez-Marco, 1991; Cope, 1996a; Liljedahl, 1994; Waller, 1998). However, Waller (1998) could not identify a synapomorphy uniquely linking the Praenuculidae with the nuculoidean families Nuculidae and Pristiglomidae. Carter *et al.* (2000) indicated that *Praenucula* is basal to the clade that contains both the superfamily Nuculoidea and the order Solemyoida, with the latter including "ctenodontids." Carter *et al.* therefore removed the Praenuculidae from the superfamily Nuculoidea and the order Nuculoida.

Praenuculid shell microstructure has been reported only for *Palaeoconcha* sp. from the Upper Ordovician Maquoketa Formation near Graf, Iowa (Mutvei, 1983). The phosphatized shell contains relict nacre tablets that are much wider than modern nacre tablets. Because gastropod and cephalopod nacre tablets from the same locality are similarly wide, secondary enlargement during phosphatization seems likely.

Praenucula faba **Liljedahl, 1994 (Figs. 1.3, 5)**

The present observations of *Praenucula faba* are based on dorsoventral acetate peels through two specimens with united valves (RMMo 15908, 25661). All sections passed from the hinge to the ventral margins. Specimen RMMo 25661 shows evidence for a dorsal, slightly submarginal, opisthodetic, simple ligament with continuous mineralization (Fig. 5). The thickness of the lamellar sublayer of the posterior ligament remains unknown; a relatively thin sublayer is hypothesized in Figs. 5.3-5.5. There is also evidence for lamellar ligament within an anterior, submarginal fossette (Fig. 5.1, 5.7). There is no evidence for a resilium.

The ventral shell margins are smooth and thinly tapering. The outer shell layer is thin and slightly reclined to nearly vertical, finely prismatic. The middle and inner shell layers and the hinge are nacreous. There is no well developed pallial myostracum.

Order Nuculoida Gray, 1824
Superfamily Nuculoidea Gray, 1824

The superfamily Nuculoidea is presently restricted to the families Nuculidae Gray, 1824, and Pristiglomidae Sanders and Allen, 1973, *i. e.*, excluding the Praenuculidae MacAlester, 1969. Sanders and Allen (1973) and Allen and Hannah (1986) differentiated the Nuculidae and Pristiglomidae on the basis of ctenidium size and structure, shape of cerebral ganglion and hindgut, and triangular or ovate as opposed to rounded shell shape, respectively. Waller (1998:17) listed three synapomorphies for the clade of Nuculidae plus Pristiglomidae: (1) heel of the foot distinct and sharply separated from the sole, (2) multiple loops in the hindgut, and (3) resilium with non-calcified central portion and calcified lateral portions containing mainly granular rather than fibrous aragonite. This last feature must now be regarded as a derived condition within the superfamily Nuculoidea, because one of the earliest nuculoideans, *Nuculoidea pinguis* (Lindström, 1880), has a mainly fibrous lateral resilium. Medially unmineralized, laterally fibrous resilia are widespread in the Palaeotaxodonta, having evolved not only within the superfamily Nuculoidea but also in various members of the superfamily Nuculanoidea Adams and Adams, 1858 (Carter, 1990).

Family Nuculidae Gray, 1824

Maxwell (1988) divided the Nuculidae into the subfamily Nuculominae Maxwell, 1988, which lacks large, radial prisms, and the subfamily Nuculinae Gray, 1824, which has such prisms. These are denticular composite prisms as defined by Carter *et al.* (1990b), *i.e.*, second-order prisms organized into first-order prisms by virtue of reflection and denticulation of the shell margins. Maxwell's

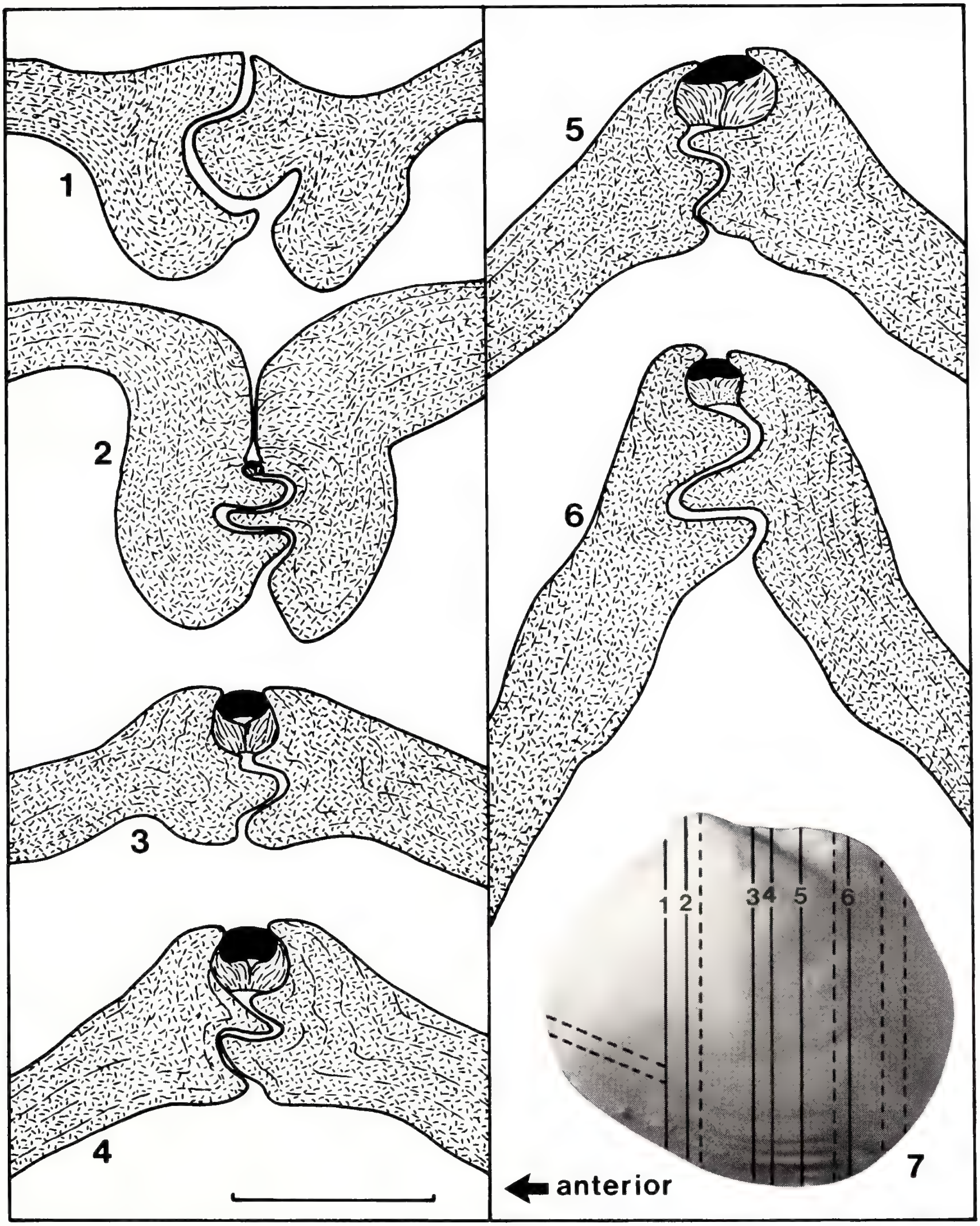

Fig. 3. Camera-lucida drawings of dorsoventral acetate peels through the hinge and ligament of *Ekstadia tricarinata* Soot-Ryen, 1964, Upper Silurian, Wenlockian, probably Mulde Formation, Gotland, Sweden, RMMo 15469 (3.1-3.6) and RMMo 15468 (3.7), both shells 8.2 mm in length. Fig. 3.7 shows the positions of illustrated sections through RMMo 15469 as numbered lines; the dashed lines represent sections that are not presently illustrated. In Figs. 3.1-3.6, irregularly oriented dashes between the growth lines represent fine CCL and/or homogeneous structure. A thin, impersistent, reclined prismatic outer shell layer is also present, but is not shown because it is too thin to be accurately represented. The dashes within the ligament fossettes (3.2-3.6) represent relict ligament fibers; the solid black areas above these dashes represent hypothesized lamellar ligament.

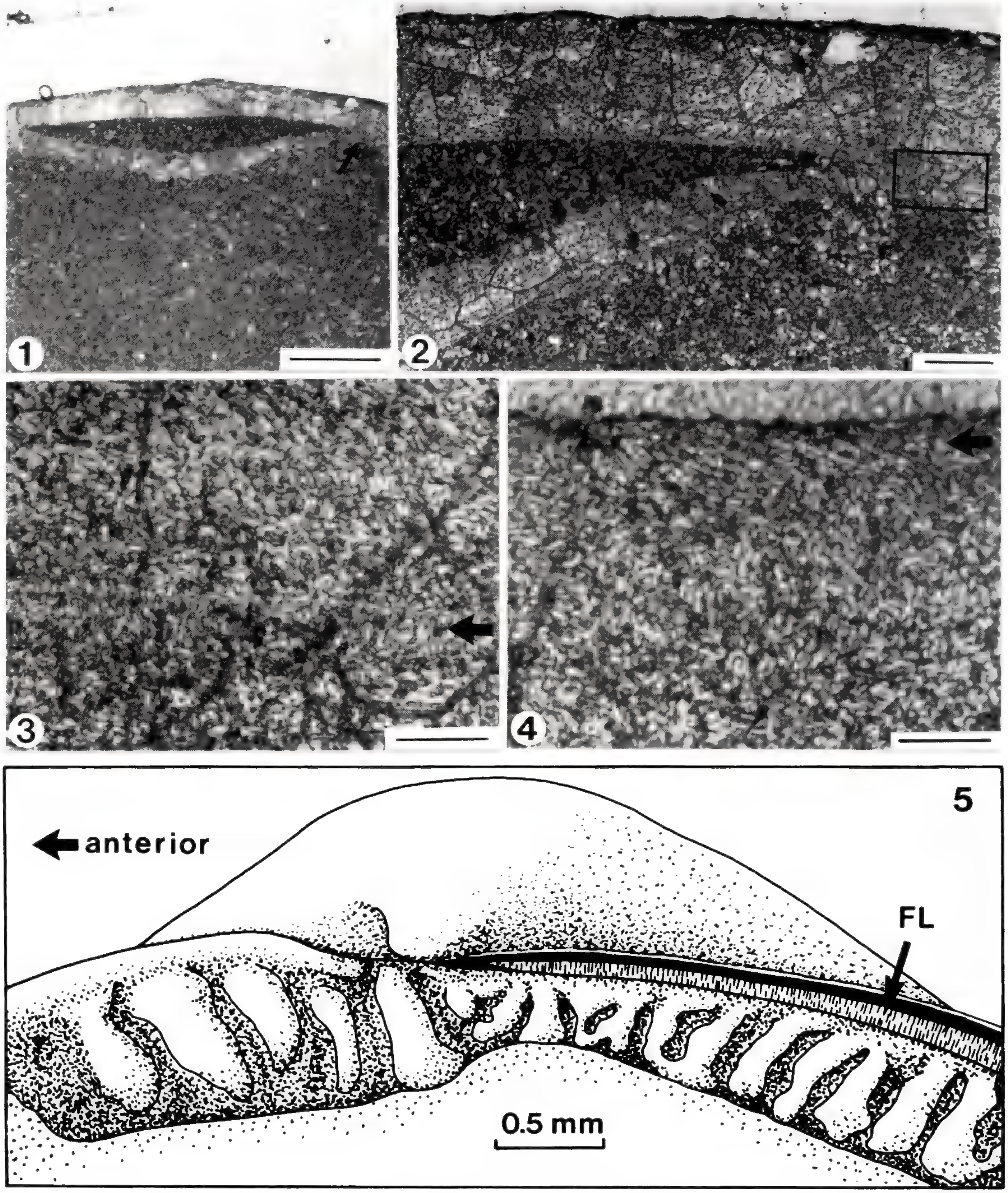

Fig. 4. *Ekstadia tricarinata* Soot-Ryen, 1964, Upper Silurian, Wenlockian, probably Mulde Formation, Gotland, Sweden, RMMo 15469. 4.1-4.3, progressively higher magnifications of an acetate peel of a dorsoventral section along the dashed line between sections 5 and 6 in Fig. 3.7, showing an interior shell blister (4.1); a thin, horizontal sublayer of irregular simple prisms (arrow in 4.3) underlain by poorly preserved crossed acicular structure (see Fig. 2.5 for a better view of the latter); Fig. 4.3 is an enlargement of the area indicated by the arrow in 4.1 and by the rectangle in 4.2; the shell exterior is up and the ventral shell margin is toward the right in all three figures; bar scales = 500 µm, 100 µm, and 25 µm, respectively. 4.4, acetate peel of a radial, vertical section near the anteroventral shell margin, showing the reclined prismatic (arrow) outer shell layer and the underlying crossed acicular (CA) middle shell layer; the shell exterior is up and the anteroventral shell margin is toward the right; bar scale = 25 µm. 4.5, reconstructed hinge and opisthodetic, submarginal, simple ligament, based on 10 dorsoventral sections through the hinge of RMMo 15469 (see Fig. 3.7 for positions of sections, using RMMo 15468) and fig. 34D of Liljedahl (1994); FL = fibrous ligament, overlain by reconstructed lamellar ligament (thick black line).

(1988) Silurian-Recent subfamily Nuculominae is presently restricted to largely nacreous nuculids without denticular composite prisms. Largely porcelaneous nuculids without denticular composite prisms are presently placed in the new Carboniferous-Recent subfamily Palaeonuculinae. The Palaeonuculinae replaced ancestral nacre with porcelaneous and matted structure in their adult stage, whereas the Carboniferous(?) or Cretaceous-Recent subfamily Nuculinae remained largely nacreous internally, and evolved denticular composite prisms. The denticular composite prisms thickened and interlocked the ventral shell margins, thereby enhancing protection against predation. The coarse, marginal denticulations in the Nuculinae differ from the marginal micropectinations present in some, but not all, Nuculominae, *e.g.*, in Devonian *Nuculoidea opima* (Hall, 1843). These micropectinations affect primarily the nacreous, inner margin of the shell, rather than the prismatic outer shell layer (Schenck, 1934; Carter, 1990:145).

Subfamily Nuculominae Maxwell, 1988

This subfamily includes *Nuculoidea* Williams and Breger, 1916, *Nuculoma* Cossmann, 1907, *Nuculopsis* Girty, 1911, *Economolopsis* Hoare, Heaney, and Mapes, 1989, *Leionucula* Quenstedt, 1930, *Ennucula* Iredale, 1931, and *Brevinucula* Thiele, 1935, among others. Keen (1969) indicated that the genus *Nuculoidea* ranges from Ordovician to Devonian, but Pojeta and Runnegar (1985) noted that resilia are unknown in Ordovician palaeotaxodonts. The earliest presently known member of the Nuculominae, and hence of the Nuculidae and the superfamily Nuculoidea, is Silurian *Nuculoidea.*

Carter (1990, p. 147) found no evidence for mineralization in the simple ligament and resilium of two Devonian species of *Nuculoidea.* Lack of resilial mineralization in Devonian *Nuculoidea* now seems unlikely, given the present observations of Silurian *Nuculoidea.* Middle Devonian *Nuculoidea* has an adult outer shell layer of vertical simple(?) prisms, reclined fibrous prisms, and irregular simple prisms, and a juvenile outer shell layer of nearly vertical to reclined, irregular simple prisms. The middle and inner shell layers are nacreous except for minor porcelaneous structure near the ligament insertion area of one species.

***Nuculoidea pinguis* (Lindström, 1880) (Fig. 6)**

Soot-Ryen (1964) and Liljedahl (1994:34) noted a small, slightly to moderately excavated resilifer and no external ligament in *Nuculoidea pinguis.* The present observations are based on dorsoventral acetate peels through three specimens with united valves. This includes 15 sections through RMMo 21914 (Figs. 6.2-6.6), 9 sections through RMMo 21913 (Fig. 6.1), and 4 sections through RMMo 15520. A symmetrical, internal resilium is present, as well as an anterior, dorsal, submarginal, lamellar ligament. Mineralization in the resilium is lateral and mainly fibrous, with granular mineralization only near the medial, unmineralized part of the ligament. The latter is not shown in Fig. 6.3 in order to illustrate the spatial distribution of the adjacent lateral mineralization. The presence of a dorsal, submarginal, anterior lamellar ligament is indicated by minute fossettes with concentrated, framboidal pyrite (Fig. 6.2). These fossettes do not extend posterior to the beaks.

The shell margins are smooth and thinly tapering. The outer shell layer is relatively thin, and consists of finely textured, nearly vertical to slightly reclined prisms. The middle and inner shell layers are predominantly nacreous. A well developed pallial myostracum is not apparent.

Subfamily Nuculinae Gray, 1824
***Nucula proxima* Say, 1822 (Fig. 7)**

The subfamily Nuculinae includes *Nucula* Lamarck, 1799, *Gibbonucula* Eames, 1951, *Lamellinucula* Schenck, 1944, *Linucula* Marwick, 1931, *Pectinucula* Quenstedt, 1930, *Pronucula* Hedley, 1902, and *Acila* Adams and Adams, 1858, among others. Nuculine shell and ligament microstructure has been studied by Schmidt (1922), Bøggild (1930), Wrigley (1946), Lucas (1952), Trueman (1952), Van de Poel (1955), Taylor *et al.* (1969), Speden (1970), Wise (1970), Kobayashi (1971), Flajs (1972), Suzuki (1983), Waller (1990), and Carter (1990). As illustrated by Recent *Nucula proxim*a, the outer shell layer in this subfamily is denticular composite prismatic, and the middle and inner shell layers are nacreous except for prismatic myostracal deposits (Fig. 7). Porcelaneous structure is absent except in a small area of fine CCL or homogeneous structure immediately below the umbones in the inner shell layer (Carter et al., 1990a:306). Pallial myostracal prisms are only locally present.

Subfamily Palaeonuculinae nov.

The subfamily Palaeonuculinae is presently named for the Group of *Palaeonucula* Quenstedt and *Condylonucula* Moore, as defined by Carter (1990:148). *Palaeonucula* Quenstedt, 1930, is designated as the type genus. Palaeonuculines differ from other nuculids in having a largely non-nacreous adult shell. The juvenile shell may be nacreous or non-nacreous. Like the Nuculominae, they lack denticular composite prisms. Palaeonuculines resemble pristiglomids in having a non-nacreous adult shell, but pristiglomids lack nacre in their juvenile stage and matted structure in their adult stage.

Bøggild (1930:276) mentioned that Middle Jurassic "*Nucula hammeri*" (presumably of DeFrance, 1825, although not so indicated by Bøggild), the type species of *Palaeonucula* Quenstedt, 1930, has a homogeneous or very indistinctly prismatic shell. Lucas

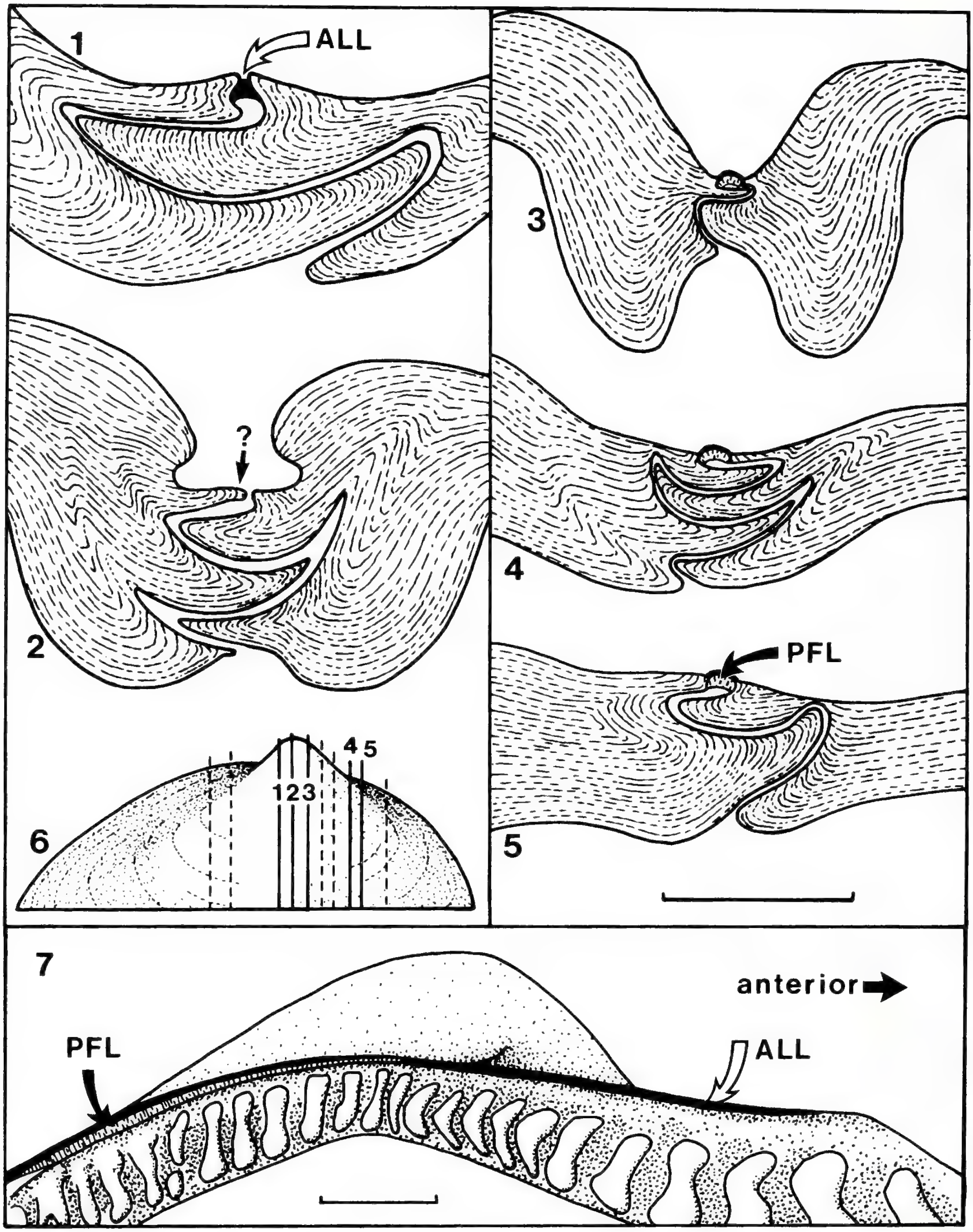

Fig. 5. Reconstructed shell and ligament microstructure of *Praenucula faba* Liljedahl, 1994, Upper Silurian, Wenlockian, Mulde Formation, Gotland, Sweden, based on camera lucida drawings of 10 dorsoventral sections through RMMo 25661 (section positions indicated by numbered lines on the left valve in Fig. 5.6; the dashed vertical lines in Fig. 5.6 indicate sections not presently illustrated; sectioned shell was 8.25 mm in length; ALL = anterior lamellar ligament, based on concentrations of framboidal pyrite; PFL = posterior fibrous ligament based on relict ligament fibers. The thickness of the lamellar sublayer of the posterior ligament, shown in Figs. 5.3-5.6 as a thick, black line, is hypothetical. The broken curving lines in 5.1-5.5 represent relict nacreous laminae. All vertical sections passed from the hinge to the ventral shell margins. The bar scale below Fig. 5.5 represents 0.5 mm and applies to sections 5.1-5.5. The bar scale for Fig. 5.7 represents 0.5 mm. The prismatic outer shell layer is too thin to be shown in these sections.

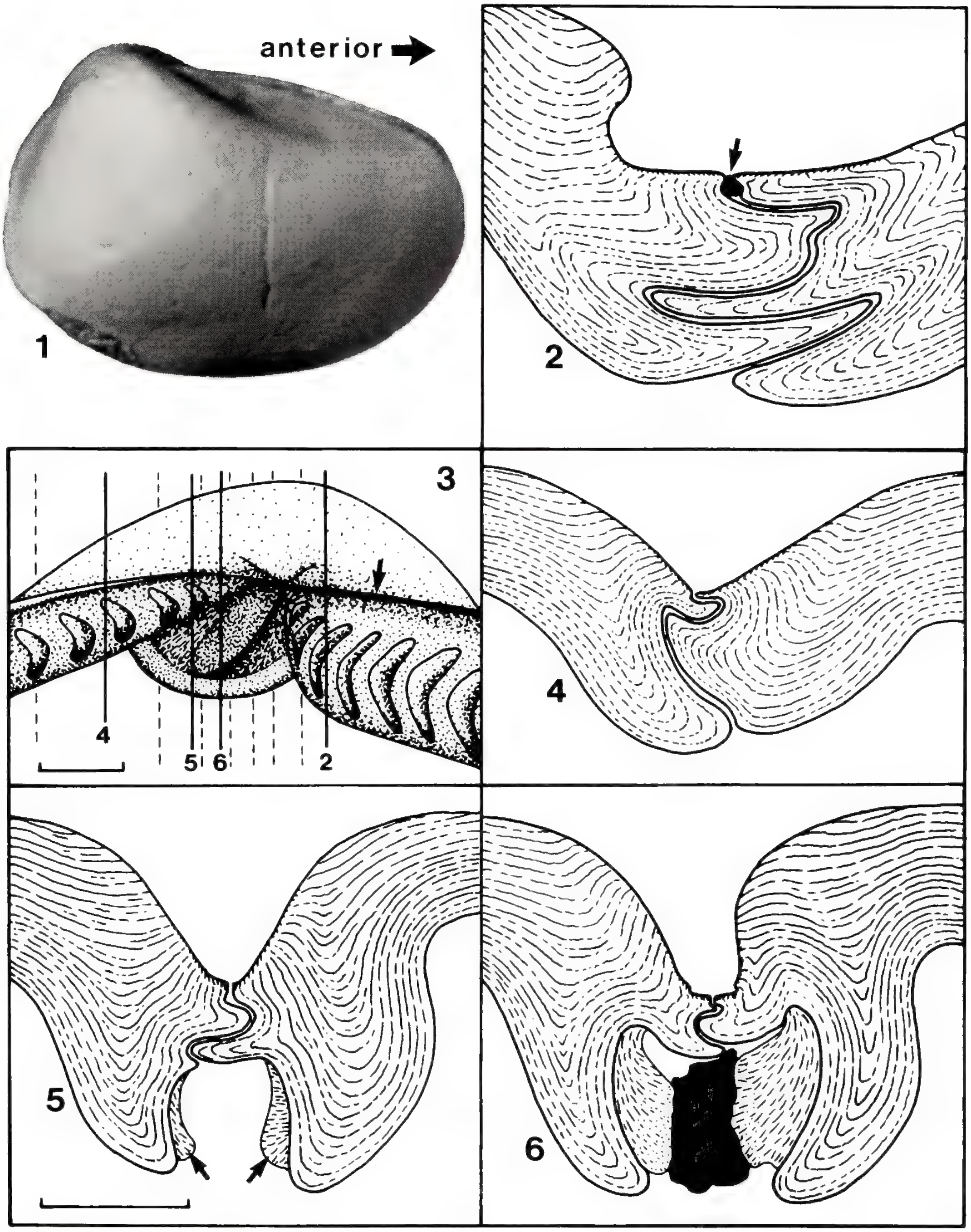

Fig. 6. Shell and ligament microstructure of *Nuculoidea pinguis* (Lindström, 1880), Upper Silurian, Wenlockian, Gotland, Sweden. 6.1, exterior of right valve, 8.2 mm in length, RMMo 21913, probably Mulde Formation; the anterior is toward the right. 6.2, 6.4-6.6, camera lucida drawings of dorsoventral sections through a shell 9.0 mm long (RMMo 21914, Mulde Formation), with section positions indicated by number in Fig. 6.3; dashed vertical lines in 6.3 show sections not presently illustrated. 6.2, dorsoventral section immediately anterior to beaks, showing submarginal, lamellar ligament (solid black, at arrow) inferred from concentrations of framboidal pyrite; the left and right valves appear asymmetrical because the section is oblique to the commissure plane. 6.4, dorsoventral section slightly posterior to the resilifer. 6.5, dorsoventral section through posterior part of resilifer, showing fibrous part of resilium (arrows). 6.6, dorsoventral section through central part of resilium, showing left and right fibrous and granular resilium separated by lamellar resilium (the latter shown by solid black area, shape and position based on concentrations of framboidal pyrite). 6.3, reconstructed hinge and ligament of a left valve; bar scale = 0.5 mm; fibrous resilium covers the surface of the resilifer, and grades from fibrous (dashes) to granular (stippled). In Fig. 6.3, the fossette for the anterior, dorsal, submarginal, lamellar ligament is shown by a thick black line (at arrow). The longer dashed lines in Figs. 6.2 and 6.4-6.6 are tracings of nacreous laminae; the shorter dashed lines near the dorsal surface of the hinge indicate the thin, finely prismatic outer shell layer. The bar scale in 6.5 represents 0.5 mm, and also applies to Figs. 6.2, 6.4, and 6.6.

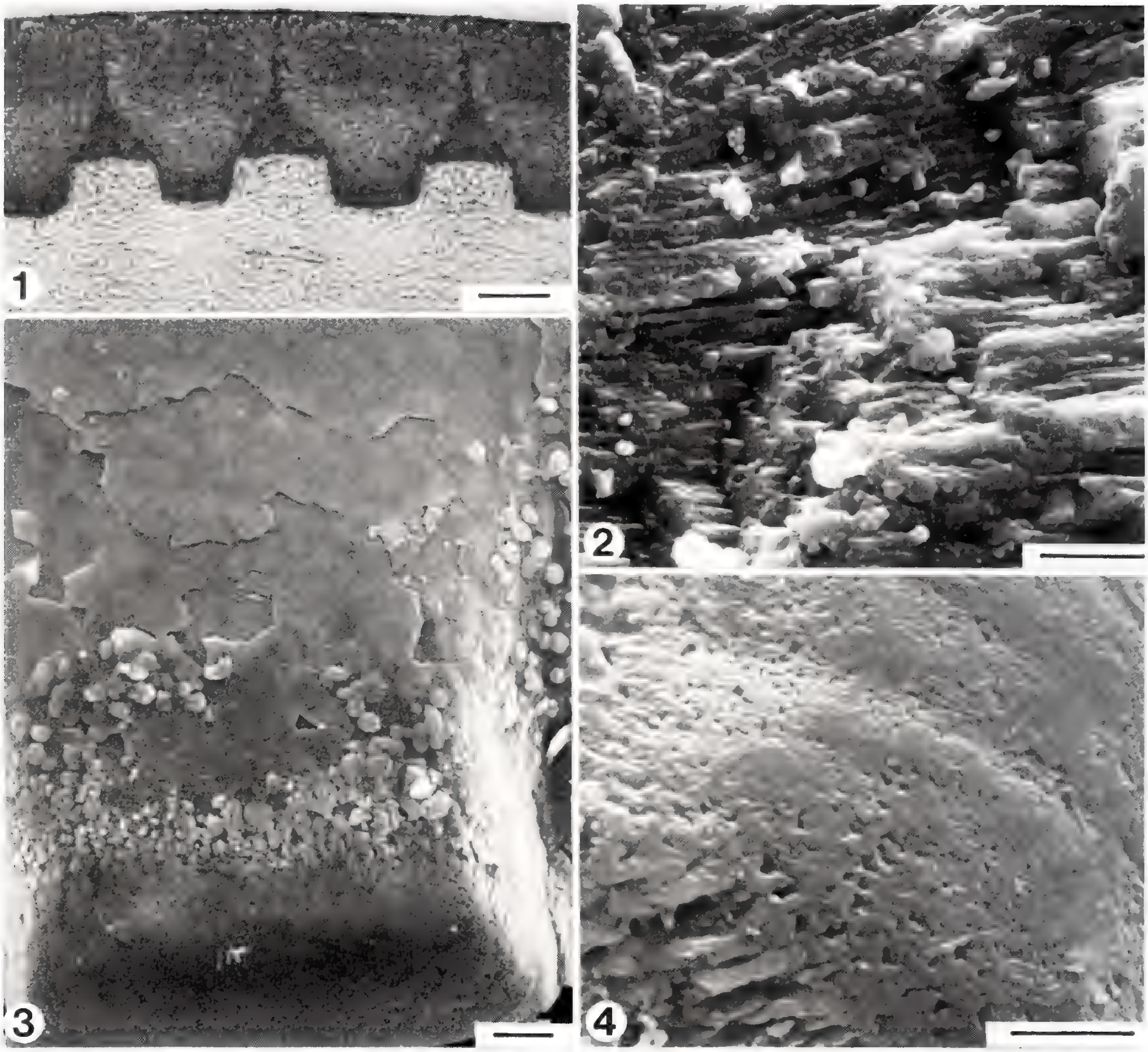

Fig. 7. Denticular composite prismatic outer layer and nacreous middle layer of Recent *Nucula proxima* Say, 1822, Long Island Sound, New York, YPM 10014. 7.1, acetate peel of a transverse, vertical section near the ventral shell margin, showing four radial, denticular composite prisms (above) and nacreous laminae (below); bar scale = 50 µm. 7.2-7.4, SEM of a radial, vertical fracture (7.2) and depositional surface (7.3, 7.4) of a single, denticular composite prism; bar scales = 5 µm in 7.2 and 7.3; bar scale = 10 µm in 7.4. In Fig. 7.3, the depositional surface of the prismatic outer layer is near the bottom of the photograph, and that of the nacreous middle layer is in the middle and upper part of the photograph; note the decrease in size of the nacre tablets toward the shell margin. Fig. 7.4 shows the depositional surface of a single denticular composite prism.

(1952) indicated that Upper Triassic *Palaeonucula strigilata* (Goldfuss, 1838) has an outer shell layer of reclined, radial fibrous prisms, a middle homogeneous layer, and an inner nacreous layer. Carter *et al.* (1990:309) examined this same species and found an outer shell layer with two sublayers: outer irregular simple prismatic to homogeneous, and inner finely irregular simple prismatic to fibrous prismatic. The middle and inner shell layers are homogeneous, but with a locally nearly matted structure that might be mistaken for nacre. Two other Triassic species of *Palaeonucula* were found by Carter *et al.* (1990a) to have largely porcelaneous shells, with an outer shell layer that varies from nearly vertical to reclined irregular simple prismatic to fibrous prismatic, to homogeneous. Upper Carboniferous *Palaeonucula* sp. cf. *P. wewokana* (Girty, 1911) has a homogeneous shell and a partially fibrous resilium. Upper Carboniferous *Palaeonucula?* cf. "*Nucula*" *subrotundata* (Girty, mss. in Morningstar, 1922) has an outer shell layer of nearly vertical, fibrous prisms locally grading into dissected crossed prisms. The rest of the shell consists primarily of homogeneous structure, but this is locally transitional to crossed acicular or fine CCL, with bands of irregular simple prisms and rare irregular CCL near the umbones (Carter, 1990).

Condylonucula maya Moore, 1977 (Fig. 8.1, 8.2)

Moore (1977) indicated that Recent *Condylonucula* lacks nacre. *Condylonucula maya* is only about 0.5 mm long at maturity, making it one of the smallest bivalves. The juvenile stage has an outer layer of slightly reclined, fibrous to irregular simple prisms, and middle and inner nacreous layers (Fig. 8.2). Later in ontogeny, the juvenile nacre is covered by irregular simple prisms (lower part of Fig. 8.2), and the middle shell layer becomes homogeneous to matted (Fig. 8.1). The matted structure is organizationally transitional between nacreous and porcelaneous, *i.e.*, retaining the laminar first-order arrangment of nacre, but having more or less homogeneous rather than tablet-like basic structural units.

Family Pristiglomidae Sanders and Allen, 1973

Allen and Hannah (1986) provided the following diagnosis for the Pristiglomidae: shell round; gills small, with markedly reduced number of short filaments; hind gut looped or coiled about both sides of the stomach. Waller (1990) noted that the pristiglomid resilium has granular lateral mineralization. Pristiglomids have not otherwise been described microstructurally.

Pristigloma nitens (Jeffreys, 1876) (Fig. 8.3)

Recent *Pristigloma nitens* has a thin, outer shell layer of radially reclined, fibrous to irregular simple prisms; a crossed acicular middle shell layer; and an inner shell layer that varies from fine CCL to irregular CCL to homogeneous (Fig. 8.3). The hinge is mostly fine CCL, but shows some crossed acicular and irregular CCL structure where it grades laterally into the umbonal part of the inner layer. Laminar microstructures, including nacre and matted structure, are absent at all ontogenetic stages.

Order Solemyoida Gray, 1840

McAlester (1969) placed the family Ctenodontidae Wöhrmann, 1893 in the order Nuculoida, and Newell (1969) placed the superfamily Solemyoidea in the order Solemyoida, subclass Cryptodonta Neumayr, 1884. Allen (1978, 1985) indicated that similarities in the form of the foot, gills, and digestive diverticula suggest a common origin for nuculoids and solemyoids. Scarlato and Starobogatov (1979) included the Nuculoida and Solemyoida in the superorder Protobranchia Pelseneer, 1889, and they assigned both the Ctenodontidae and Praenuculidae to the superfamily Ctenodontoidea. Pojeta (1988) tentatively placed *Ctenodonta* Salter, 1852, and its allies in the nuculanoidean family Malletiidae, and he regarded *Ctenodonta* as ancestral to the order Solemyoida, which he placed in the Palaeotaxodonta. Liljedahl (1994) similarly placed *Tancrediopsis*, a close relative of *Ctenodonta*, in the Malletiidae. Waller (1990) defined the order Solemyoida on the basis of various anatomical features and loss of nacre, and he indicated that the Ctenodontidae and Solemyidae have similar ligament nymphs. Waller (1998) later separated the Nuculanoidea from the clade of Nuculoidea plus Solemyoidea, and he placed the family Ctenodontidae within the superfamily Solemyoidea. Waller (1998) listed several synapomorphies for the Solemyoidea, including sulfur-oxidizing bacterial symbiosis, posterior adductor muscle smaller than the anterior adductor muscle, and several soft anatomical features. Cope (1996b, 1997) transferred the Solemyoida to the subclass Lipodonta Iredale, 1939, although he maintained a palaeotaxodont origin for the group.

The phylogenetic analysis of Paleozoic bivalves by Carter *et al.* (2000) resolved the orders Nuculoida *s.s.* and Solemyoida as sister groups, and, within the Solemyoida, resolved *Tancrediopsis* basal to the clade of *Ctenodonta* plus *Acharax*. Synapomorphies identified for the Solemyoida, inclusive of the "ctenodontids" *Tancrediopsis* and *Ctenodonta*, include: triangular posteroventral shell margin; greatly elongated shell anterior with nearly parallel dorsal and ventral margins; opisthogyrate beaks; concavo-convex anterior palaeotaxodont dentition; and a wide, external, parivincular ligament. This list of synapomorphies will undoubtedly be modified as additional solemyoids, such as *Psiloconcha* Ulrich, 1894, *Dystactella* Hall and Whitfield, 1872, and *Clinopistha* Meek and Worthen, 1870, are added to the analysis.

The order Solemyoida is presently defined to include anteriorly or anteroventrally elongated, parivincular palaeotaxodonts such as *Tancrediopsis, Ctenodonta*, and *Acharax* and their solemyid, nucinellid, and manzanellid descendants. Relatively derived solemyoids may retain a parivincular ligament (*e.g.*, solemyids), or they may replace it with a simple ligament (*e.g.*, nucinellids), thereby reverting to the plesiomorphic condition for the Palaeotaxodonta.

Solemyoidean shell microstructure has been studied by Bøggild (1930), Beedham and Owen (1965), Taylor *et al.* (1969), Speden (1970), Kobayashi (1971), and Carter (1990). At least some Paleozoic solemyoideans were largely nacreous, whereas modern solemyoideans are porcelaneous-prismatic. Kobayashi (1971) reported nacre in an Oligocene *Solemya (Petrasma) velum* Say, 1822. Shell and ligament microstructure has not previously been described for "ctenodontids" such as *Tancrediopsis.*

Tancrediopsis gotlandica (Soot-Ryen, 1964) (Fig. 9)

According to Liljedahl (1994), *Tancrediopsis gotlandica* should be regarded as the type species of both *Tancrediopsis* Beushausen, 1895, and *Gotodonta*

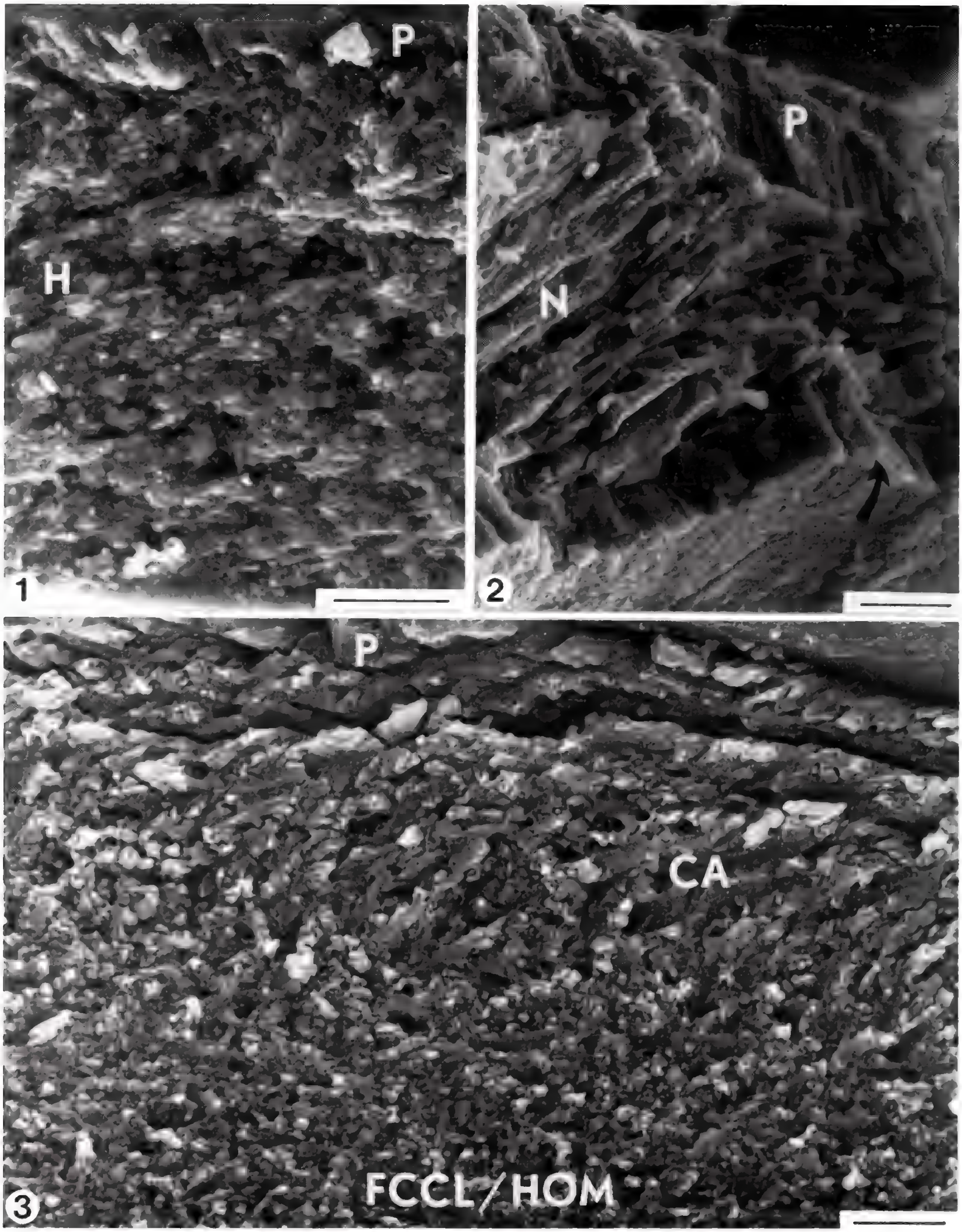

Fig. 8. Shell microstructure of predominantly porcelaneous nuculoideans. 8.1, 8.2, *Condylonucula maya* Moore 1977, collected by Dr. Donald Moore at the type locality, Chancanab Lagoon, 2 meters depth, Cozumel, Mexico (UNC 15236); SEM of dorsoventral, radial fractures; the shell exterior is up and the ventral margin is toward the right. 8.1, reclined prismatic outer shell layer (P) underlain by homogeneous to matted structure (H) near the adult ventral shell margin. 8.2, umbonal part of shell, showing reclined prismatic outer shell layer (P) and nacreous middle and inner layer of juvenile shell (N), the latter covered interiorly by a later ontogenetic irregular simple prismatic inner shell layer (at arrow); the inner depositional surface appears near the bottom of the photograph. 8.3, *Pristigloma nitens* (Jeffreys 1876), 2644 meters depth, Atlantic Ocean, 8° 28.8'N, 56° 4.5'W; SEM of ventral, radial, section, acid-etched and then treated with sodium hypochlorite to remove the organic matrix; shell exterior is up and ventral shell margin is toward the left; epoxy embedding block appears at far upper right; radially reclined prismatic outer shell layer (P) and crossed acicular (CA) middle shell layer, grading inward into fine CCL to homogeneous, inner shell layer (FCCL/HOM). Bar scales = 5 µm.

Soot-Ryen, 1964. Liljedahl (1994) indicated that *Gotodonta* and *Tancrediopsis* are based on the same species because the first designation of the type species of *Tancrediopsis* (by Cossmann, 1897) is invalid, as it does not agree with the original generic diagnosis. The type species of *Tancrediopsis* should instead be *Nucula sulcata* Hisinger, 1841, a junior homonym of *N. sulcata* Bronn, 1832. *N. sulcata* Hisinger was renamed by Soot-Ryen (1964) *Gotodonta gotlandica*, the type species of *Gotodonta*. McAlester (1969:N228) and Liljedahl (1994) regarded *Gotodonta* and *Praectenodonta* Philip, 1962, as synonyms.

Tancrediopsis gotlandica has an external, opisthodetic, parivincular ligament with a thick, strongly dorsally arched fibrous sublayer elevated by distinct nymphs (Fig. 9.2, 9.3, 9.6). The ligament fibers are oriented horizontally near the exterior of the ligament, but vertically near its inner part (Fig. 9.3, 9.6). The nymph is nacreous except for a thin, finely prismatic ligostracum where the fibrous ligament attached. The fibrous ligament did not extend anterior to the beaks, but the presence of anterior, submarginal fossettes suggests an anterior lamellar ligament (Fig. 9.5, 9.6). The fossettes are slightly asymmetrical, with the right fossette slightly higher and flatter than the left (Fig. 9.5). It remains uncertain whether the anterior fossettes contained lamellar ligament, because their framboidal pyrite is only slightly more concentrated than between the adjacent hinge teeth (Fig. 9.5).

The ventral and posterior shell margins are smooth and thinly tapering. The shell is moderately thick, with closely approximated shell margins all around. The outer shell layer is microstructurally distinct from the underlying nacre, but its microstructure appears largely featureless in acetate peels, with faint indications of irregular simple prisms and reclined fibrous prisms (Fig. 9.4). Not present are relatively large, regular simple prisms such as occur in *Acharax (Nacrosolemya) trapezoides* (Meek, 1874) (Carter, 1990:175, fig. 18A) and modern solemyoideans (Beedham and Owen, 1965; Taylor *et al.*, 1969:71; Carter and Lutz, 1990, pl. 20).

The middle and inner shell layers of *Tancrediopsis gotlandica* are nacreous, without a well-differentiated pallial myostracum. *T. gotlandica* differs from *Acharax trapezoides* and Recent *Solemya* in lacking porcelaneous structure in its ligament supports and major shell layers, but it resembles *A. trapezoides* in having nacreous middle and inner shell layers.

DISCUSSION

Cambrian bivalved molluscs probably evolved from minute, laterally compressed monoplacophorans similar to *Anabarella* Vostokova, 1962, *Watsonella* Grabau, 1900 (= *Heraultipegma* Pojeta and Runnegar, 1976), and *Pseudomyona* Runnegar, 1983 (Runnegar and Pojeta, 1974; Morris, 1979; MacKinnon, 1982, 1985; Runnegar, 1996; Kouchinsky, 1999). However, it remains uncertain whether the Cambrian molluscan bivalve grade is monophyletic or diphyletic. The largely calcitic, Middle Cambrian *Tuarangia* MacKinnon, 1982, may have been derived from a largely calcitic, foliated monoplacophoran similar to *Pseudomyona*, whereas Early Cambrian *Pojetaia* Jell, 1980, and *Fordilla* Barrande, 1881, most likely evolved from aragonitic ancestors similar to *Watsonella. Tuarangia* is clearly bivalved in the sense that it has distinct ligament insertion areas, differentiated left and right beaks, and possibly also separate anterior and posterior adductor muscle scars (Hinz-Schallreuter, 1995). However, *Pseudomyona* is commonly cited as its closest relative on the basis of similarities in shell shape and foliated microstructure (MacKinnon, 1982, 1985; Runnegar, 1983, 1985; Runnegar and Bentley, 1983; Runnegar and Pojeta, 1992). The hypothesis of an ancestral relationship between *Watsonella* and "fordilloids" has recently been strengthened by the discovery that *Watsonella* had a divided larval shell (Dzik, 1994:267), as well as certain microstructures in common with Early Cambrian *Pojetaia* and *Fordilla* (see Kouchinsky, 1999). The phylogenetic analysis by Carter *et al.* (2000) placed *Pseudomyona* and *Tuarangia* between *Watsonella* and *Pojetaia*, with these four genera comprising a paraphyletic grade. Their cladogram did not resolve *Pseudomyona* and *Tuarangia* as monophyletic, thereby leaving open the possibility that their foliated microstructure is homoplasious.

Recent studies of *Anabarella* and *Watsonella* have provided important new insights into microstructural comparisons with *Pojetaia runnegari* Jell, 1980. Runnegar (1983) and Kouchinsky (1999) demonstrated from steinkern impressions that the prismatic outer shell layer of *Anabarella* and *Watsonella* consisted of thin, flattened, columnar prisms with variably developed interprismatic matrices. These interprismatic matrices were probably thick near the lateral and subapical shell margins, judging from non-preservation of this prismatic layer on these parts of the steinkern margins (Kouchinsky, 1999, fig. 5). Impressions of similar outer-layer prisms can be seen on steinkerns of the Middle Cambrian, laterally compressed monoplacophoran *Mellopegma georginensis* Runnegar and Jell, 1976 (Runnegar, 1983, fig. 4D), a possible descendant of *Anabarella* or *Watsonella*. Kouchinsky (1999) showed that juvenile shells and the apical and dorsal parts of the adult shells of *Anabarella* and *Watsonella* consisted entirely of this prismatic outer shell layer. The dorsal, median part of the shell in *Anabarella* and *Watsonella* was therefore transitional between a "pseudoligament" as defined by Carter *et al.* (2000), *i.e.*, morphologically specialized for dorsal flexing but not completely microstructurally

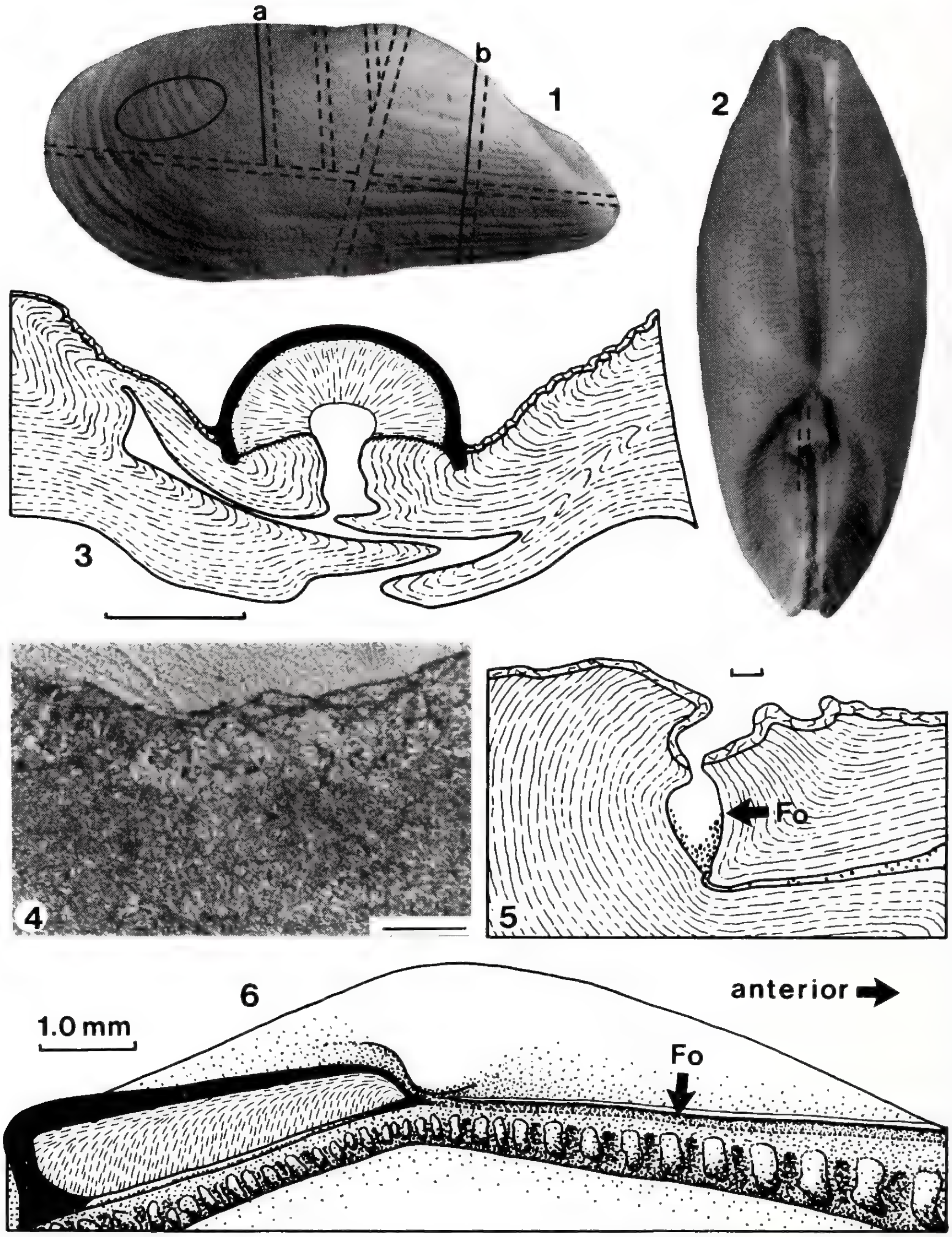

Fig. 9. Shell and ligament microstructure of the "ctenodontid" *Tancrediopsis gotlandica* (Soot-Ryen, 1964), Upper Silurian, Wenlockian, Mulde Formation, Gotland, Sweden, RMMo 15761 (Figs. 9.1-9.2) and RMMo 15768 (Figs. 9.3-9.5). 9.1, 9.2, left valve and dorsal view of united valves of a shell 25.2 mm in length; lettered lines indicate positions of illustrated sections for RMMo 15761 or 15768; dashed lines are sections not presently illustrated; specimen RMMo 15768 was also sectioned twice parallel to the commissural plane, through the hinge dentition (section positions not presently shown). 9.3, camera-lucida drawing of dorsoventral acetate peel through the parivincular ligament and hinge at section "b" in 9.1; the thickness of the lamellar outer sublayer of the ligament (thick black line) is guessed from concentrations of framboidal pyrite in the ligament grooves flanking the fibrous sublayer of the ligament; lines within the body of the shell represent nacreous laminae; a very thin, prismatic ligostracum separates the ligament from its nymph; the outer shell layer is represented by a thin, exterior band flanking the nymphs; bar scale = 1 mm. 9.4, acetate peel of a dorsoventral section near the posteroventral shell margin at section "b" in 9.1, showing the outer shell layer (above, with microstructure poorly preserved) and the underlying middle shell layer (showing very faint, relict nacreous laminae); the shell exterior is up and the posteroventral shell margin is toward the left; bar scale = 50 µm. 9.5, camera lucida drawing of dorsoventral section through the anterior hinge at section "a" in 9.1, showing the outer shell layer (upper band with irregular lines); the underlying nacreous hinge; and left and right fossettes (Fo) partially filled with framboidal pyrite (black spots); because framboidal pyrite also occurs between the hinge teeth, its presence does not, in this instance, necessarily indicate the former presence of unmineralized, lamellar ligament; bar scale = 100 µm. 9.6, medial hinge and opisthodetic, parivincular ligament, reconstructed from sections and from pl. 2, fig. 8 of Soot-Ryen (1964); Fo = fossette anterior to beaks, possibly (?) with lamellar ligament.

differentiated from the adjacent shell plates, and a true ligament, which is so differentiated.

Kouchinsky (1999) demonstrated that the "nacreous" structure that Runnegar (1983:126) reported for *Anabarella* is a combination of structures that Kouchinsky called "spiny" and "stepwise" textures. Similar microstructures occur in *Watsonella*. Kouchinsky (1999) referred these textures to the crossed microstructure category of Carter *et al.* (1990b). Indeed, the spiny texture locally shows a complex crossed lamellar arrangement (Kouchinsky, 1999, fig. 4E). However, the stepwise texture and other parts of the spiny texture are better regarded as laminar structures, *i.e.*, with first-order laminae oriented parallel or nearly parallel with the depositional surface (Carter *et al.*, 1990b). Some parts of the spiny texture in *Anabarella* resemble "*Sepia* sp. laminar structure" as defined by Carter *et al.* (1990b, fig. 14). The stepwise texture varies from lamello-fibrillar (= "type 2 nacre" of Mutvei, 1970) to large tablet, imbricated nacre. The latter structure is strikingly similar to the imbricated structure comprising the middle and inner shell layers of *Pojetaia runnegari* and *Fordilla troyensis* Barrande, 1881. These two "fordilloids" differ from *Anabarella* and *Watsonella* in depositing large tablet, imbricated nacre to the exclusion of complex crossed lamellar and lamello-fibrillar structures in their middle and inner shell layers. As illustrated by Runnegar and Bentley (1983, fig. 4G), the outer shell layer in *P. runnegari* consisted of flat, polygonal prisms with thick, interprismatic organic matrices, *i. e.*, similar to those comprising the outer shell layer of *Anabarella* and *Watsonella*. The fact that steinkern margins of *Pojetaia* show incipient imbricated nacre, and not prisms separated by thick organic matrices, probably reflects early postmortem disintegration of the latter, as in *Anabarella* and *Watsonella*. The large tablet, imbricated structure in *Anabarella, Watsonella, Pojetaia*, and *Fordilla* should be classified as a form of nacre because of its laminar first-order organization, tablet-like structural subunits, and presumed aragonitic mineralogy. Large tablet, imbricated nacre is unknown among modern bivalves, but small-tablet, imbricated nacre is approximated in the early juvenile stage of *Condylonucula maya* (Fig. 8.2). The association of imbricated nacre with minute shells in Early Cambrian molluscs and Recent *Condylonucula* suggests that tablet imbrication reflects a biomechanical or depositional constraint related to small shell size. This imbricated stacking contrasts with the vertical stacking of columnar nacre, which associates with fast-growing surfaces, and with the horizontal to slightly imbricated stacking of sheet nacre, which associates with relatively slow-growing surfaces (Wise, 1970). The decrease in tablet size near the shell margins of *P. runnegari* and *F. troyensis* (see Runnegar and Pojeta, 1992, fig. 1) recalls the similar diminution in tablet size near the ventral margins of *Nucula proxima* (Fig. 7.3).

Runnegar (1983, fig. 10F) illustrated relict columnar prisms in the opisthodetic ligament of *Pojetaia runnegari*. He suggested that these prisms are homologous with the prismatic structure that he believed comprised the shell plates, but with proportionally more organic matrix. Runnegar's (1983, fig. 10D,E) thin section through the calcite-replaced ligament shows no evidence for differentiated outer lamellar and inner, strongly mineralized sublayers. If the ligament in *Pojetaia* consisted of periostracum and a single, weakly mineralized, columnar prismatic layer, as Runnegar suggests, then the opisthodetic, simple ligament of early palaeotaxodonts may have evolved by adding a sub-periostracal, lamellar sublayer through modification of the dorsoposterior shell repair response, as suggested by Waller (1990, 1998), and by prolonging the period of growth in width of underlying ligament fibers to continue after the polymerization of their surrounding protein matrix, thereby increasing the opening moment and mineralization of the inner sublayer.

The flat, polygonal, exterior prisms in *Pojetaia runnegari* differ from the finer, radially reclined prisms in the outer shell layer of *Praenucula, Nuculoidea, Ekstadia*, and many other early or middle Paleozoic, wholly aragonitic bivalves. However, polygonal prisms co-occur with fine, radial prisms in the outer shell layer of the Devonian malletiid *Palaeoneilo filosa* (Conrad, 1842) (Carter, 1990, fig. 10B).

Interestingly, Middle Cambrian *Mellopegma georginensis* shows evidence for small-tablet sheet nacre similar to modern molluscs (Runnegar, 1983, fig. 4c). If Cambrian monoplacophorans transformed large tablet, imbricated nacre into modern nacre, then Cambrian "fordilloids" probably had a similar evolutionary potential. Cambrian "fordilloids" are in fact microstructurally varied. Geyer and Streng (1998) found that Middle Cambrian *Pojetaia sarhroensis* Geyer and Streng, 1998 differs microstructurally from Early Cambrian *P. runnegari*. Instead of flat, polygonal prisms in the outer shell layer, it has finely textured prisms, and instead of large tablet, imbricated nacre, it has "irregular prismatic" structures interiorly. The latter resemble crossed lamellar and irregular complex crossed lamellar structures in later porcelaneous bivalves (Geyer and Streng, 1998, fig. 4). However, these porcelaneous microstructures in *P. sarhroensis* are probably convergent on porcelaneous cardiolariids such as *Ekstadia* and porcelaneous malletiids such as *Palaeoneilo* Hall and Whitfield, 1869. The available evidence suggests that cardiolariids and malletiids evolved from nacreous palaeotaxodonts (Carter, 1990).

The hypothesis by Runnegar (1983, 1985) that *Pojetaia runnegari* and *Fordilla troyensis* had entirely prismatic shells is no longer tenable. Runnegar (1985, fig.

2C,D) illustrated a thin section through a recrystallized shell of *P. runnegari*, which reportedly shows prisms with uniformly parallel sides. Their shapes do not agree with his interpretation that the prisms increased in diameter from exterior to interior by geometric selection. The "prism" boundaries resemble calcite fracture planes locally developed in the homogeneous part of the outer shell layer in a Devonian *Palaeoneilo filosa* (Conrad, 1842) (Carter, 1990, fig. 10C). Columnar prisms in bivalve shells do not have imbricated depositional surfaces, whether these are slightly reclined, non-denticular composite prisms in trigonioids; radially elongate simple prisms in solemyids; aragonitic, regular simple prisms in pholadids; or calcitic simple prisms in pinnids (Carter and Lutz, 1990, pls. 20, 24, 29, 49). The closely spaced, transverse marks that Runnegar and Pojeta (1992:118) identified as casts of aragonite fibers in the "prisms" of *P. runnegari* and *F. troyensis* appear to be the structural subunits of large, imbricated nacre tablets. Similar structural units comprise the lamello-fibrillar structure in *Anabarella* (see Kouchinsky, 1999, fig. 2E), the imbricated nacre in *Watsonella* (see Kouchinsky, 1999, fig. 3H), and the sheet nacre in some Recent bivalves (Mutvei, 1983, fig. 3B).

The relationship of "fordilloids" to post-Cambrian bivalves remains problematic. Among the more recently published perspectives on this issue, Runnegar and Bentley (1983) suggested that *Pojetaia* gave rise to praenuculid palaeotaxodonts, whereas *Fordilla* gave rise to mytiloids, orthonotids and pholadomyoids. Pojeta (1985) presented a similar phylogeny in which *Pojetaia* and *Fordilla* gave rise to palaeotaxodonts and isofilibranchs, respectively. Cope (1996a) stated that *Pojetaia* is a palaeotaxodont, and he later (1997) included *Fordilla* in this group. Geyer and Streng (1998:87) placed *Pojetaia* and *Fordilla* in the Praenuculidae because these taxa resemble juveniles of later praenuculids. On the other hand, Waller (1990), Runnegar and Pojeta (1992), and Runnegar (1996) suggested that fordilloids comprise a sister group to crown group bivalves, although Runnegar and Pojeta (1992) kept open the possiblity that *Pojetaia* and *Fordilla* are the earliest palaeotaxodonts and isofilibranchs, respectively. Carter *et al.* (2000) noted that the "pretaxodont" hinge teeth in *Pojetaia* and *Fordilla* differ from palaeotaxodont *s.s.* hinge teeth. *Pojetaia* has at most four stout, broad based teeth in shells reaching 2.25 mm in length (Geyer and Streng, 1998, table 1), whereas post-Cambrian palaeotaxodonts commonly have at least six relatively sharply defined teeth in shells as small as 1.0 mm, with additional taxodont teeth in larger shells. Carter *et al.* (2000) suggested that *Pojetaia* and *Fordilla* are basal to crown group bivalves, and that these "fordilloids" represent a paraphyletic grade. According to their phylogenetic analysis, crown group bivalves are characterized by reduction in nacre tablet size as well as changes in pedal and adductor musculature, continuity of the pallial line, and ligament mineralization. Because of the presence of large tablet, imbricated nacre in *Anabarella* and *Watsonella*, the retention of this distinctive microstructure in Early Cambrian *Pojetaia* and *Fordilla* should not be regarded as a synapomorphy for the Fordilloida, but a plesiomorphy for the Bivalvia.

The discovery of strong resilial mineralization in *Nuculoidea pinguis* was unexpected, because Carter (1990) found no evidence for resilial mineralization in two Devonian species of *Nuculoidea*. It now appears likely that the Devonian resilia were less well preserved, or that their lateral resilial mineralization had already evolved from mainly fibrous to mainly granular, with the latter being more difficult to identify as relicts in diagenetic calcite. The ligament in *N. pinguis* resembles that in modern nuculoideans except for having mainly fibrous rather than mainly granular lateral mineralization. This is compatible with Waller's (1990:60) hypothesis that the nuculoidean resilium represents a submerged, opisthodetic simple ligament. However, resilia apparently evolved convergently in nuculoidean and nuculanoidean palaeotaxodonts (McAlester, 1964; Pojeta, 1978).

Praenuculids are microstructurally and ligamentally suitable ancestors for early nuculoids such as *Nuculoidea pinguis*. Because *Praenucula* was nacroprismatic and had an anterior, submarginal, lamellar ligament, submergence of its posterior, simple fibrous ligament would have produced a taxon similar to *Nuculoidea*. *Praenucula* may have also given rise to nacroprismatic "ctenodontids" such as *Tancrediopsis* by elevating its posterior ligament on nymphs. The parivincular ligament in *T. gotlandica* is strikingly similar to that in the Upper Carboniferous acharacid solemyoidean *Acharax (Nacrosolemya) trapezoides*. Both species have short, weakly projecting nymphs supporting a barrell-shaped, fibrous ligament with horizontally and vertically oriented fibers (Carter, 1990:172, fig. 17D; horizontal ligament fibers misidentified as "lamellar" ligament). *Tancrediopsis* differs from *Acharax* in having well developed, palaeotaxodont hinge teeth. However, Hoare *et al.* (1979, pl. 2, fig. 15) illustrated a specimen of *A. trapezoides* with a "chondrophore" consisting of a tooth-like, inverted V-shaped structure just ventral and posterior to the beaks, and Carter (1990:177) observed crenulations on the medial hinge of this species. Rather than a chrondrophore, these structures may represent vestiges of palaeotaxodont teeth. *T. gotlandica* differs from *A. trapezoides* and modern solemyids in having nacreous rather than predominantly porcelaneous nymphs. However, *Tancrediopsis, A. trapezoides*, and modern solemyids might be similar in having an anterior, asymmetrical, lamellar ligament. In *Solemya*, the anterior, lamellar ligament inserts onto a small yet distinct, longitudinal ridge just inside the dorsal anterior margin of the right valve, and onto the distal or inner edge of the dorsal anterior margin of the left valve (Carter, 1990:174). A similar longitudinal ridge occurs just inside the dorsal anterior margin of the right valve in *A. trapezoides*. The dorsal margin of the left valve of *A. trapezoides* lacks this ridge, but has an area of porcelaneous structure on the inner margin of this valve, just anterior to the beaks. This arrangement matches the porcelaneous structure in the longitudinal ridge on the margin of the right valve, as well as the porcelaneous structure in its parivincular nymph, suggesting an association with ligament attachment. The dorsal anterior shell margins of *A. trapezoides* are otherwise nacreous and prismatic. *T. gotlandica* has slightly asymmetrical, anterior fossettes but, as noted previously, it is not certain that these contained lamellar ligament.

Because solemyoideans share close common ancestry with "ctenodontid" palaeotaxodonts, the order Solemyoida should be retained in the subclass Palaeotaxodonta.

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Comparison of microgrowth pattern in *Margaritifera margaritifera* shells from south and north Sweden

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Abstract: Shells of the pearl mussel *Margaritifera margaritifera* were collected from two Swedish unpolluted or moderately polluted rivers: the Vramsån River, situated in the southernmost part of Sweden (Scania) and the Välijoki River, situated in the northernmost part of Sweden, 100 km above the Polar Circle. In southern Sweden the climate is mostly maritime and the mean annual temperature is about +8°C, whereas in northernmost Sweden the climate is mostly continental and the mean annual temperature is about -1°C.

The annual growth rate and microgrowth pattern in the shells from these mussels, living in climatologically very different environments, were analyzed and compared. The microgrowth pattern, with growth acceleration and retardation zones, is the same within each population and specific for each year, but different between the two populations in the study. The shells from the Vramsån River population have 160 ± 30 microlamellae, whereas the shells from the Välijoki River population have 100 ± 30 microlamellae. The number of lamellae corresponds to the number of days with water temperatures higher than 5°C in each locality, suggesting diurnal growth periodicity of the shells. The growth rate is higher and the deposited microlamellae are thicker in younger individuals, being about 2-5 μm. Older mussels deposit thinner microlamellae of 170-400 nm or even less. This difference in thickness makes it difficult to compare young individuals with old ones.

Key Words: Mollusca, Bivalvia, *Margaritifera*, microgrowth, microlamellae

The periodicity of growth increments has been studied in bivalves, barnacles, trees, fish otoliths, and cephalopod statoliths. It has been shown that this periodicity is annual, monthly, fortnightly, diurnal, and semidiurnal and is explained by direct influences of environmental factors and endogenous rhythms (Pannella and Macclinock, 1968; Pannella, 1971, 1980; Fritts, 1972; Higgins, 1980; Kennish *et al.*, 1980; Dodge and Vaisnys, 1980; Richardson *et al.*, 1980; Mosegaard, 1986; Crisp, 1989).

Changes in the external environment induce physiological changes that result in altered concentrations of metabolic end products and, in this way, determine changes in Ca deposition in otoliths of fishes and in shells of molluscs, creating specific growth patterns. These internal growth patterns have been proven to be useful in ecological and palaeontological studies for assessing the effects of various biological and environmental stress (Pannella and Macclinock 1968; Rhoads and Pannella, 1970; Farrow, 1972; Kennish and Olsson, 1975), archaeological studies for reconstructing settlement patterns of prehistoric hunter-gatherers (Coutts, 1970; Koike, 1973), and geophysical studies for defining changes in the rate of the earth's rotation (Berry and Baker, 1968; Pannella *et al.*, 1968; Rosenberg and Runcorn, 1975).

The growth of bivalve shells has been the subject of intensive research in ecology and environmental monitoring for many years. Most of the research has been centered around the examination of the macroscopic growth features in relation to environmental problems of marine and freshwater ecosystems. The present study is focused on more detailed and higher-resolution records of shell growth in the freshwater unionid *Margaritifera margaritifera*.

In the winter period of temperate climates, shell growth ceases more or less, owing to the low temperature of the water and limited food supply (Bayne and Widdows, 1976). During this period, a very distinct etch-resistant band, "dark band," is deposited, also called the winter line. A similar etch-resistant band is deposited if the edge of the mantle has been damaged mechanically or chemically, forming the disturbance line.

The annual growth rate of the shell is not constant. Etch-resistant bands, indicating growth retardation, alternate with less etch-resistant bands, indicating growth acceleration. These bands have different thickness forming a specific pattern of growth. By studying this growth pattern and the growth rate of the shell, which reflects the life-

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history of the bivalve, the environmental changes can be monitored.

MATERIAL

For the present study shells of the pearl mussel *Margaritifera margaritifera* from two Swedish rivers (Fig. 1) were collected (Table 1).

From the River Vramsån, living specimens were collected between 1989 and 1994. In 1994 specimens were collected during several seasons of the year: in the spring (April), in the summer (July), and in the autumn (October). The age of the collected specimens varies between 15 and 85 years.

From the River Välijoki, living specimens were collected in October 1997. The age of these specimens varies between 22 and 103 years (Table 1).

The River Vramsån

The River Vramsån situated in Scania, southern Sweden, is only moderately affected by human activities, such as farming. The pH of the water is around 7.0 and it is stable due to the calcareous bedrock that increases the alkalinity of the water to >10 mmol/l (Bernes and Grundsten, 1992). The total amount of phosphorous is more than 50 µg/l which indicates a nutrient-rich water. Nutrient-rich water is probably caused by leakage of nutrients from the surrounding, easily-weathered soils as well as fertilization in connection with agricultural activities. These activities are typical for southern Sweden where large areas have been used for agriculture an extended period of history. (Bernes and Grundsten, 1992).

The River Välijoki

The River Välijoki is situated between two lakes in the northernmost part of the Sweden (Norrbotten) above the Polar Circle, about 1700 km from the River Vramsån. The pH is around 7, the alkalinity of the water is >10 mmol/l and the total amount of phosphorous is less than 25 µg/l, which indicate that this river is relatively unaffected by human activities (Bernes and Grundsten, 1992).

The Climate

The two localities were chosen for environmental studies for two reasons: (a) the water is relatively unpolluted and (b) the climate is very different. In southern Sweden the climate is mostly maritime and the mean annual temperature is about 8°C, while in northern Sweden the climate is mostly continental and the mean annual temperature is about -1°C (Raab and Vedin, 1995).

The length of the seasons is different, as well as the length of the growing period. In the south of Sweden the spring and summer begin almost two months earlier (in March) than in the north (in May). On the other hand, the autumn and winter in southern Sweden begin about two months later (in October and in December, respectively), than in northern Sweden (in August and in October, respectively). The length of the growing period, which is the average number of days with mean temperature over +5°C, is 210 days in the south and 120 in the north (Raab and Vedin, 1995).

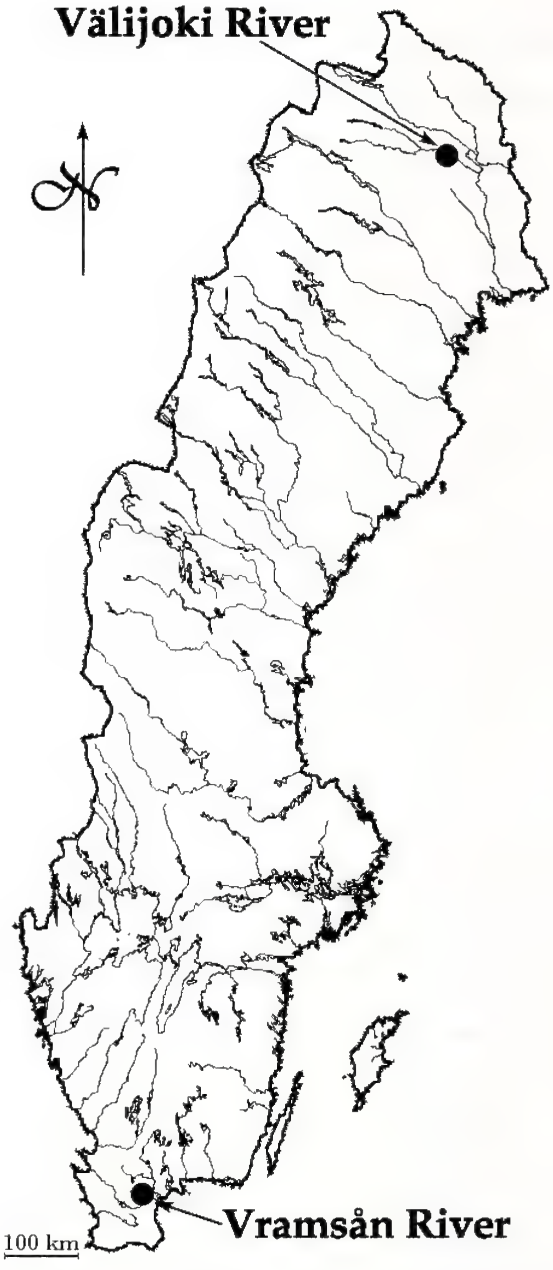

Fig. 1. Map of localities.

Table 1. Material used in the present study.

Locality of collection	Date of collection	No. of individuals	Age range (years)
River Vramsån, S Sweden	1989-1994	30	15-85
River Välijoki, N Sweden	1997	10	22-103

The amount of precipitation is also different, ca 900 mm in the south and 500 mm in the north, in the south mainly as rain and in the north mainly as snow (except between May and September when it rains) (Raab and Vedin, 1995).

The number of days with snow cover is 50 in the south and 200 in the north. The first day with snow cover is around 1st December in southern Sweden but around 10th October in northern Sweden. The last day with snow-cover is around 25 March in southern Sweden but around 15 May in northern Sweden. Snow melting is an important factor influencing the water of rivers. The waterflow increases dramatically while the pH of the water is decreasing in connection with the snow melting in spring. This occurs in March in southern Sweden and May-June in northern Sweden for a period of two to three weeks. The effects of the snow melting are more evident in the north because of the abundance of snow (Raab and Vedin, 1995).

For microgrowth studies, years with contrasting weather conditions were chosen. These years are: 1993, 1989, 1987, and 1986. In 1993 the winter was warm in the whole country. In the spring the weather was changeable. High summer temperatures, 26-28°C, occurred in the end of April in southern Sweden; it was also warm in northern Sweden. In the late summer and autumn the weather was cold and changeable particularly in southern Sweden.

In 1989 the winter was unusually warm, and spring and summer were also warm in the whole country with low precipitation, but the autumn was cold and rainy. In 1987 the winter was cold, particularly in northern Sweden where the temperature fell to -48°C. The spring and summer were cold particularly in northern Sweden, with high precipitation over the whole country. In 1986 the winter was cold particularly in southern Sweden, with unusually low temperatures down to -29°C. The spring was cold mainly in southern Sweden, 2-3°C colder than normal. An unusually warm May in the whole country made the snow melt very quickly, producing overflows.

METHODS

The shells were cut with a diamond saw from the umbo to the ventral edge, perpendicularly to the winter lines. Thin sections were prepared at the cutting plane and etched for 20 minutes with a 1:1 mixture of 25% glutaraldehyde and 1% acetic acid to which alcian blue had been added and heated to 50°C. The age of each shell was determined by counting the annual growth increments under a light microscope. To study the microgrowth pattern, a polished shell section was prepared for each bivalve and etched with the same mixture of glutaraldehyde and acetic acid for exactly 5 minutes. The best results were obtained when sections were cut exactly perpendicular to the winter lines. These sections were studied with a scanning electron microscope (SEM). NIH-Image program was used to compare the patterns of annual growth rates. This program is developed by Wayne Rasband at the National Institutes of Health and is available on http://rsb.info.nih.gov/nih-image/index.html site.

In order to study the variations of the widths of microlamellae in one and the same individual, the shell was also cut in two other directions: acute angle to the winter lines in the anterior part of the shell, and wide angle to the winter lines in the posterior part.

RESULTS AND DISCUSSION

Variations of annual growth rate

In general, the annual growth rates of shells from the two rivers under study are similar. This suggests that the different length of the growth season does not influence the shell size.

Detailed growth curves based on measurements of annual growth increments in old individuals (about 75 years old) are different for the two localities. In the 1960s the shells from the River Välijoki had a higher growth rate than those from the Vramsån River. In the 1970s the growth rate is higher in shells from the Varamsån River than those from the Välijoki River (Fig. 2).

The differences in growth rates are related to differences in temperatures of the growth season. Thus, in the 1960s the summer temperature was lower than normal in southern Sweden, but higher than normal in northern Sweden. In the 1970s the summer temperature was normal in southern Sweden, but lower in northern Sweden.

In 1989 shells from both rivers had a low growth rate, and several growth-disturbance lines occur in shells from the River Vramsån, possibly caused by a cold autumn and lack of precipitation in spring and summer.

In 1987 shells had a high growth rate in the Vramsån River but a very low growth rate in the Välijoki River. This can be explained by the cold spring and summer in northern Sweden.

As a contrast, in 1986, the growth rate was very low in shells from the Vramsån River and high in shells from Välijoki River. This was probably caused by the particularly cold spring in southern Sweden, 2-3°C colder than normal.

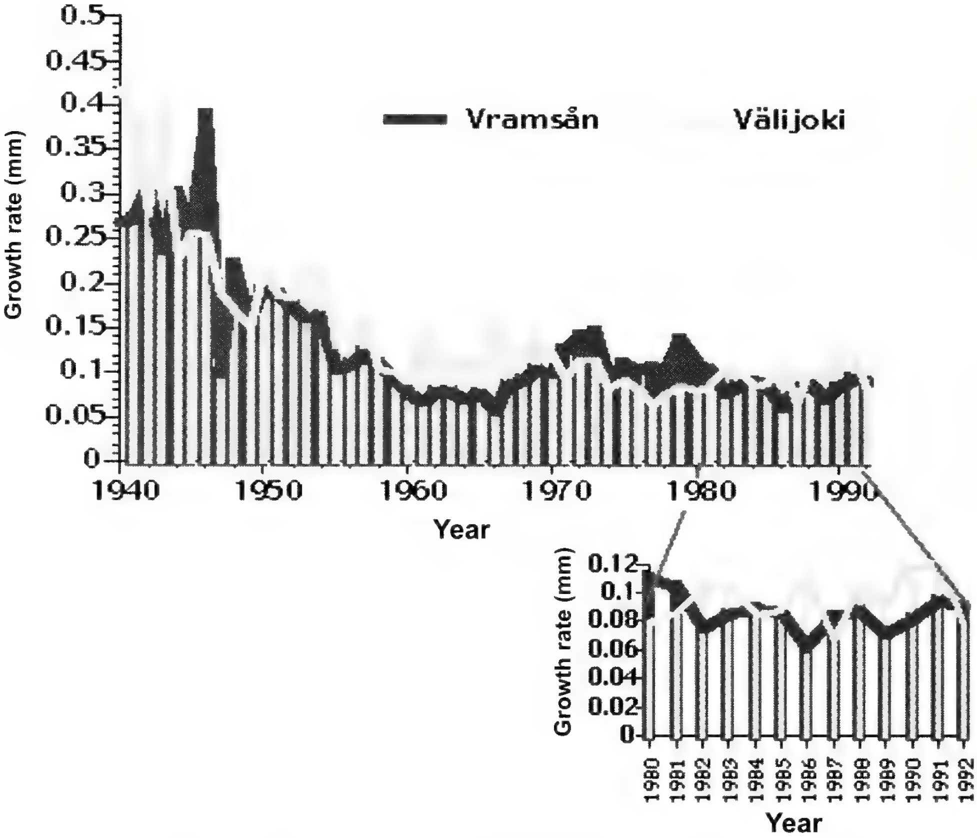

Fig. 2. Diagram of the annual growth rate averaged from measurements of three, about 75 year old shells, from the River Vramsån and the River Välijoki, respectively.

Variations of microgrowth pattern within one shell

The microgrowth pattern is best visible in the prismatic shell layer and was therefore analyzed only in the annual growth increments of this layer.

The shells show the same pattern in all three cutting directions and in both valves of the same shell (Fig. 3).

It was found that the microgrowth pattern is best visualized in sections cut perpendicularly to the winter lines. In sections with other cut directions, the microlamellae are thinner and more compact, which may explain the poor etching of these sections. The quality of the etching is also dependent on the cutting angle in relation to the long axes of the prisms. The best results are in sections cut parallel to the long axis of the prisms. In figure 3 the cutting plane is not parallel to these axes, and despite use of the same etching technique, the microgrowth pattern is indistinct.

A tendency of compression of the microlamellae within one and the same annual growth increment in the same polished section of the shell was also observed (Fig. 4). The microlamellae are thicker at the boundary with the nacre and thinner and more compressed at the outer shell edge.

The microgrowth pattern within a population

Studies of Koike (1973, 1980, and 1986) described daily growth increments in the marine mussels *Meretrix* and *Mercenaria* respectively. She found that boundaries between adjacent increments appear as narrow etch-resistant ridges or growth lines. SEM microphotographs show that the aragonite rods in these ridges are “especially dense;” X-ray analysis indicates that the ridges are rich in Ca but poor in Na (Koike, 1980). According to Rosenberg and Runcorn (1975), the growth lines (= etch-resistant ridges) are formed when the calcification rate decreases.

The *Margaritifera* shells in the present study have also narrow inter-daily, etch-resistant ridges with a dense structure. Etching with sodium hypochlorite solution and in a plasma etching device (low temperature ashing) clearly indicates that the ridges are poor in organic matter (Dunca and Mutvei, 1996). Probably, this is the situation in the etch-resistant disturbance and winter ridges. This in contrast to the anoxic theory by Lutz and Roads (1980), which explains the formation of growth lines as a result of decalcification of the $CaCO_3$ in the shell at the interface between mantle and shell during anoxic conditions.

The annual growth rate of the shells in each chosen

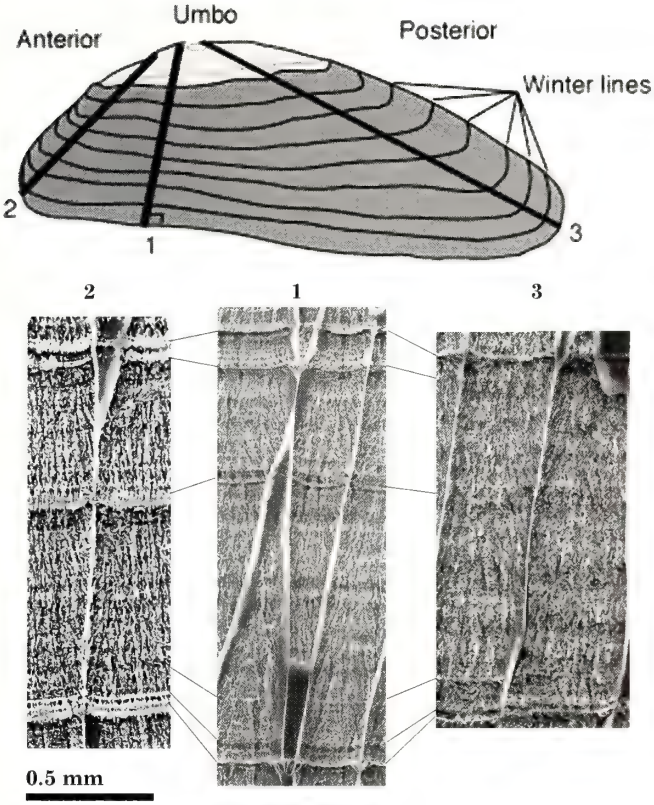

Fig. 3. Cutting directions in a unionid shell: 1- in the middle part of the shell at right angles to the winter lines; 2- in the anterior part of the shell; 3- in the posterior part of the shell.

year has a specific pattern of growth acceleration and growth retardation as seen in the zones of microlamellae.

The number of microlamellae in each annual growth increment indicates a diurnal periodicity of shell growth both in southern and northern Sweden. The shells from the south have 160 ± 30 microlamellae in each annual growth increment, which corresponds to the number of days with water temperatures higher than 5°C, and the length of the growing season from the end of April to the end of October. The shells from the north have about 100 ± 30 microlamellae in each annual growth increment, which is close to the number of days with water temperatures higher than 5°C, and the length of the growth season from the end of May to the end of September.

During the summer period the growth rate is higher, indicated by thicker microlamellae, ca 2.5 µm (Fig. 5 A).

The higher growth rate can be explained by higher metabolic rates owing to the optimal temperatures, above 10°C, and good food supply which make it possible to deposit larger aragonite crystals (Wada, 1961). At the beginning and the end of the growth season, as well as in older bivalves (over 40 years) the growth rate is lower and the deposited lamellae are much thinner, 170-400 nm (Fig. 5 B).

The microlamellae are thicker, indicating higher growth rate, in the annual increments before sexual maturation (Fig. 6 A). After the sexual maturation the microlamellae are thinner, under 1 µm, which makes the growth pattern more compact and forms in some parts more pronounced etch-resistant ridges (Fig. 6 B).

The number of microlamellae within one and the same annual increment is the same both in a young and an old individual. This means that both young and old individuals have the same diurnal rhythmicity of $CaCO_3$ deposition in the shell and only the crystal size and the density of $CaCO_3$ varies. Periods of growth retardation are recorded also during the summer. These may be caused by reproduction periods, short periods with low temperatures, and/or deficiencies in food supply. The patterns of growth acceleration and retardation are the same in shells from one and the same population. In older shells this pattern can be traced by using sequences of different ages as shown in figure 7. It seems that the microlamellae are thinner and more compact in older individuals. The changing microgrowth pattern with age creates difficulties in comparing young and old individuals. The similarities in microgrowth pattern can be revealed only by comparing individuals with similar age. Comparing shells of different ages demonstrates the tendency of the lamellae thinning with age (Fig. 7). Counting the microlamellae is difficult and the accuracy is ± 30 lines within one year.

The season of the growth has been established in shells collected at different dates by counting the microlamellae deposited after the last winter line. Shells collected 12th April had not begun to grow after the winter cessation. Shells collected 25th May had deposited ca 20 ± 5 microlamellae, and those collected 7th July had deposited 1/3 of the annual growth increment comprising ca 60 ± 10 microlamellae (Fig. 8).

In a 20 year old shell collected the 31st August 1989, 3/4 of the annual growth increment was deposited. The growth pattern of this shell is similar to the growth pattern of a 15 year old shell collected from the same population in 1994, except that 30 ± 5 microgrowth lamellae were missing before winter growth cessation (Fig. 9).

Comparison of microgrowth pattern between southern and northern Sweden

In young shells (15-30 years old) collected from southern and northern Sweden, the microgrowth pattern is different, and the number of microlamellae is lower in shells from the north. The thickness of the microlamellae seems to be the same within the same age group (Fig. 10).

The growth of the shells from northern Sweden is more uniform and less disturbed than those from southern Sweden. Individuals at the same age collected from the

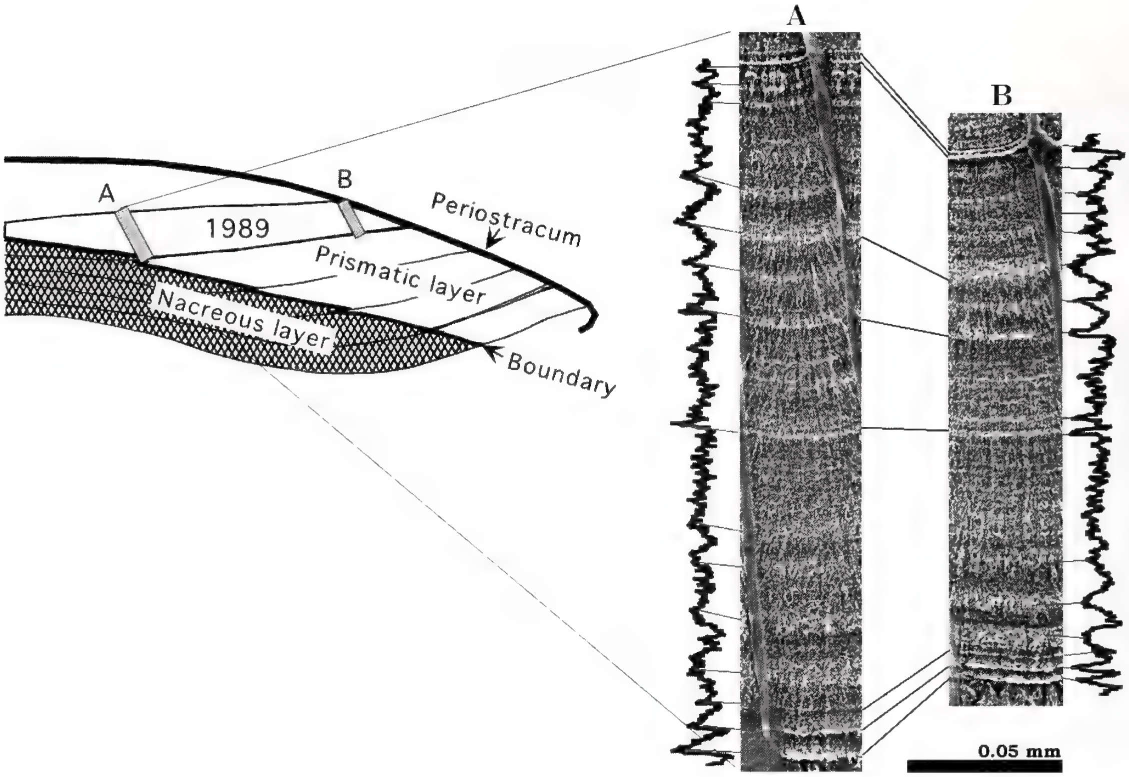

Fig. 4. The compression of microlamellae within one and the same annual growth increment of the year 1989 in a 30 year old shell from the Vramsån River. A. Near nacre boundary; B. Near the shell edge. The gray scale curves show the differences in pattern of these two profiles.

south and north have some similarities in the microgrowth pattern. In both populations the growth retardation zones occur mostly in spring and autumn and the acceleration zones occur in summer, but the succession of these zones is different (Fig. 10).

By comparing the microgrowth pattern with daily temperatures the growth retardation zones correspond to minima in temperatures, particularly when temperature differences are pronounced (Fig. 11, Fig. 12). The number of microlamellae coincides with the number of days with air temperatures higher than 5°C (Fig. 13). However, statistical analysis must be done in order to demonstrate the relationship between daily air temperature and the number of microlamellae. This is a subject for future studies.

In figure 11 the scale of the temperature curve is fixed by the date of collection (31st August) and it begins with the period with temperatures higher than 5°C. In the autumn several periods of cold days correspond to several growth retardation zones. This suggests that during these periods the growth has ceased for more than a day. The cold periods alternate with warmer periods when the shell growth starts again. All shells from southern Sweden have these, more pronounced, growth retardation zones in the autumn while the shells from northern Sweden have only one etch-resistant winter line. In the north the low temperatures come suddenly and they stay until the spring.

All these observations suggest that the main factor influencing the shell growth is the local temperature.

The influence of the temperature may be direct or indirect: higher temperatures accelerate the metabolic rate and a higher $CaCO_3$ deposition, and/or regulation of the food supply (Bayne and Widdows, 1976). It is likely that both factors occur at the same time, which underlines the major role of the temperature in the growth processes of bivalve shells. Similar conclusions can be drawn by experiments with marine bivalves (Gabbott and Bayne, 1973) and fish otoliths (Mosegaard, 1986).

This study is based on bivalve shells collected from rivers relatively unaffected by human activity, but what happens with the bivalve shells from highly polluted rivers? Do they have a distinct microgrowth pattern? Do we see the influence of temperature in the microgrowth pattern in these shells or is it replaced by the influence of the high rate of pollution?

In further studies it will be interesting to compare the growth pattern of bivalve shells from different polluted rivers and to try to find a correlation with other factors influencing the growth in these rivers other than temperature.

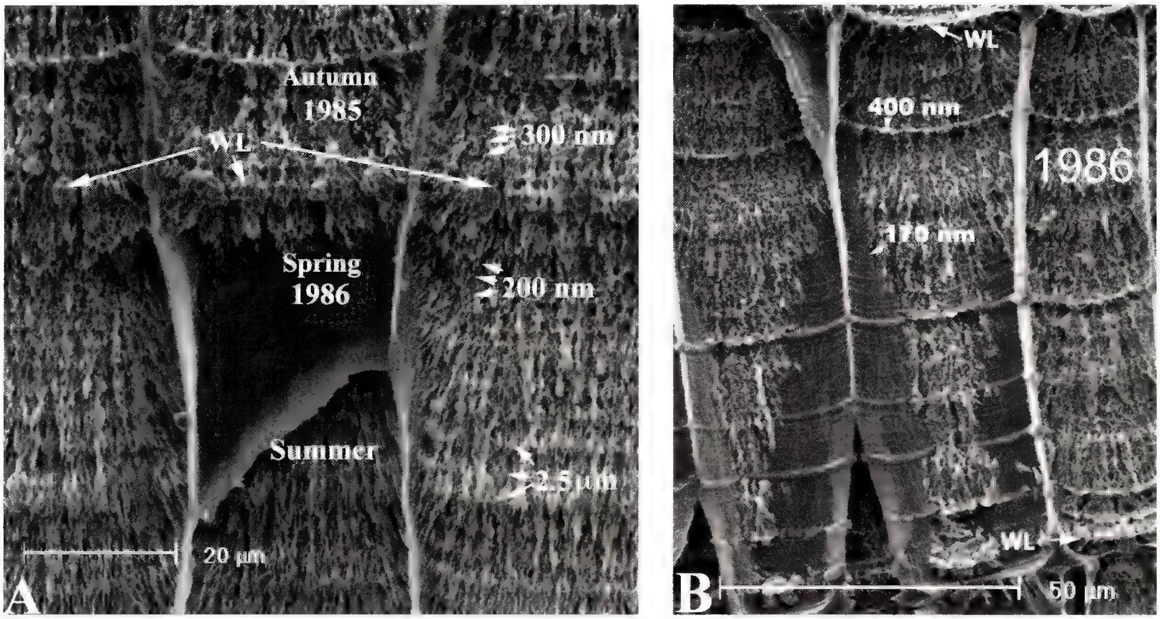
Autumn 1985
WL
300 nm
Spring 1986
200 nm
Summer
2.5 µm
20 µm
A
WL
400 nm
1986
170 nm
WL
50 µm
B

Fig. 5. A. Lamellae deposited in spring and autumn in a 14 year old shell from the River Vramsån; B. Annual increment of a 40 year old shell from the River Vramsån. WL-winter line.

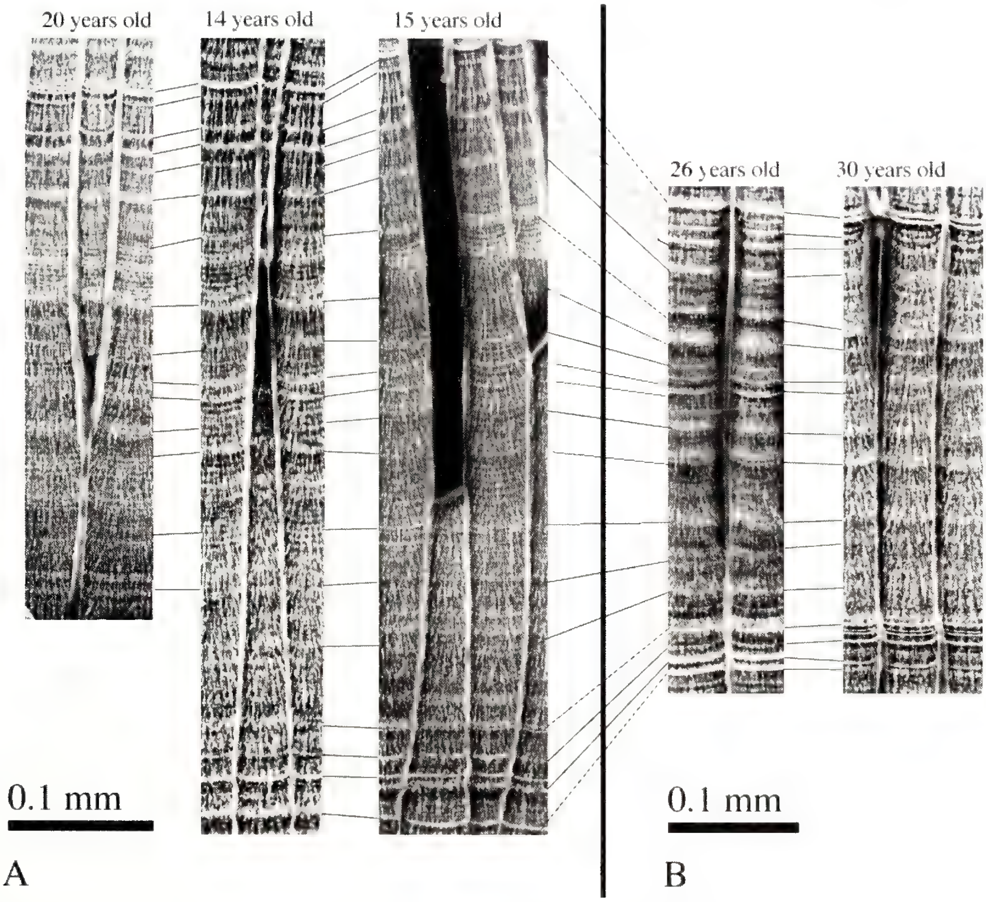
20 years old
14 years old
15 years old
26 years old
30 years old
0.1 mm
0.1 mm
A
B

Fig. 6. A. Comparison between the growth patterns in three young shells before sexual maturation (11-20 year old) in the 1989 year increment; B. Comparison between the growth patterns in two young bivalves after sexual maturation (26-30 year old) in the 1989 year increment.

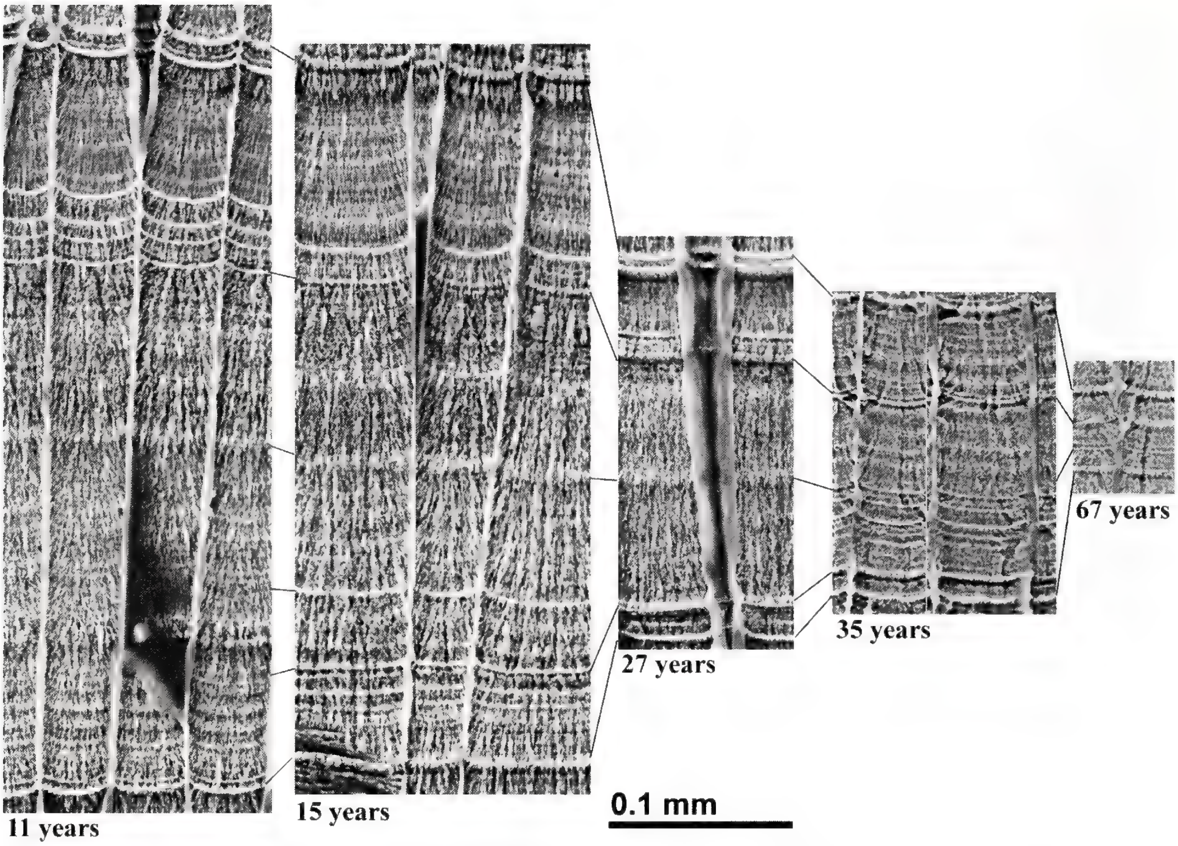

Fig. 7. Sequence of microgrowth pattern of 1986 annual increment in shells from the Vramsån River at different ages.

The study of microgrowth pattern in bivalve shells can be developed to become a powerful tool for reading the environmental archives imprinted in these shells.

CONCLUSIONS

Margaritifera shells from one and the same population have a similar microgrowth pattern of annual increments.

At younger stages the growth rate is higher by a deposition of thicker microlamellae, ca 2.5 µm thick. As it ages, the bivalve deposits thinner lamellae, ca 300nm in thickness, but the number of microlamellae remains constant.

Shells from different populations have different microgrowth patterns of annual increments.

The number of microlamellae coincide with the number of days of the growth season in each locality. The growth retardation zones within one and the same annual increment correspond to minima of daily temperatures. This suggests that the main factor influencing the shell growth is the local temperature. The temperature may influence the shell growth directly by regulating the bivalve metabolism and/or indirectly by regulating the food supply.

ACKNOWLEDGMENTS

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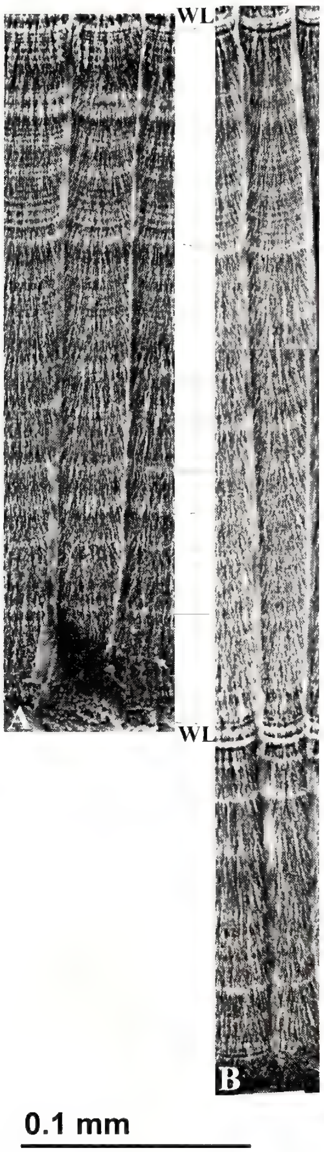

Fig. 8. Comparison between the patterns of annual growth increment for year 1993 in shells collected at different dates from the Vramsån River. A. 14 year old shell collected 12th April, B. 14 year old shell collected 7th July. WL - winter line.

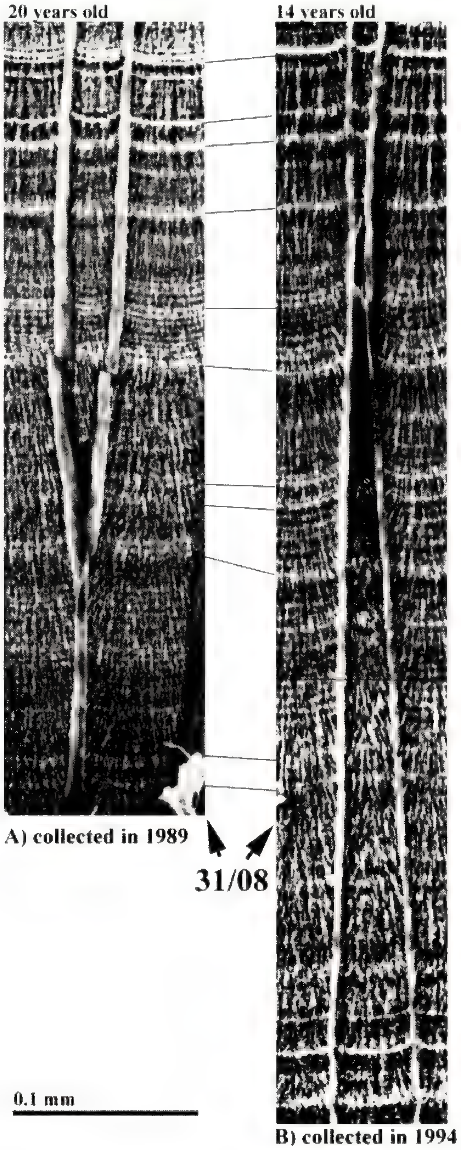

Fig. 9. The microgrowth pattern of the year 1989 in two bivalves collected: A) in 1989, August 31st (indicated) and B) in 1994.

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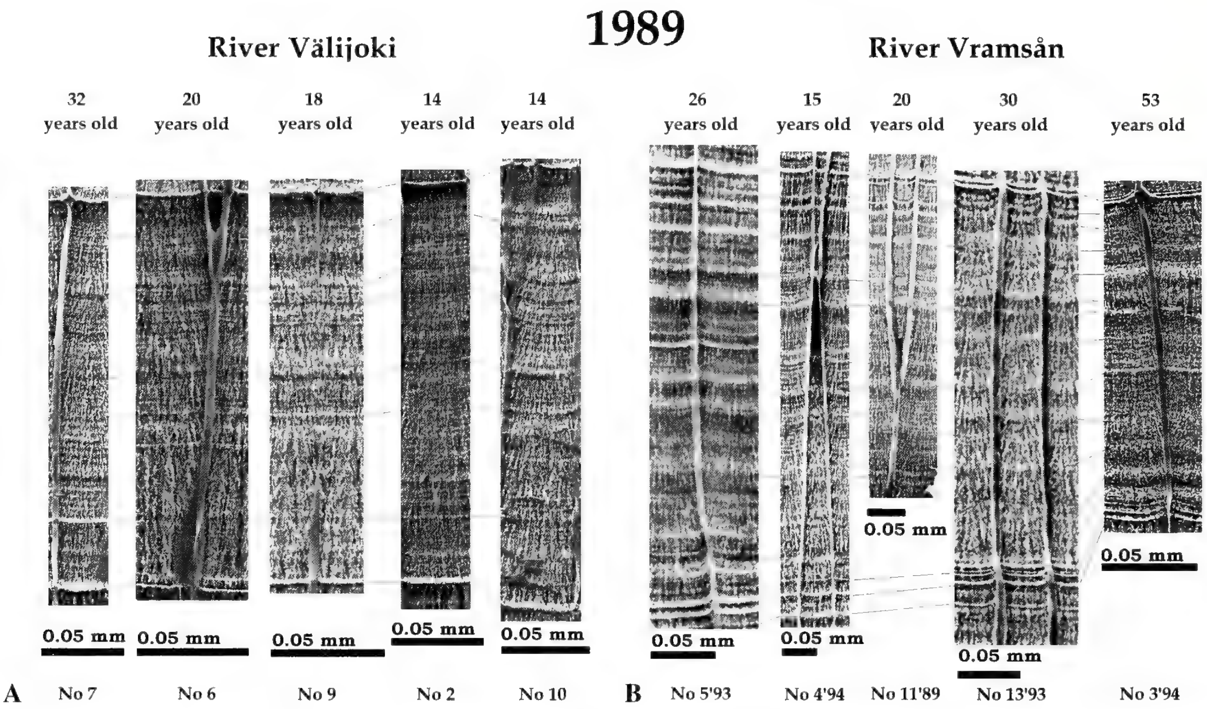
1989
River Välijoki
River Vramsån
32 years old
20 years old
18 years old
14 years old
14 years old
26 years old
15 years old
20 years old
30 years old
53 years old
0.05 mm
A
No 7
No 6
No 9
No 2
No 10
B
No 5'93
No 4'94
No 11'89
No 13'93
No 3'94

Fig. 10. The microgrowth pattern of the annual growth increment of 1989 compared between two *Margaritifera* populations A) from the Välijoki River, north Sweden, B) from the Vramsån River, south Sweden. Note that the pattern of growth acceleration and retardation is different between the two localities; however the annual growth rate is similar in the same age group.

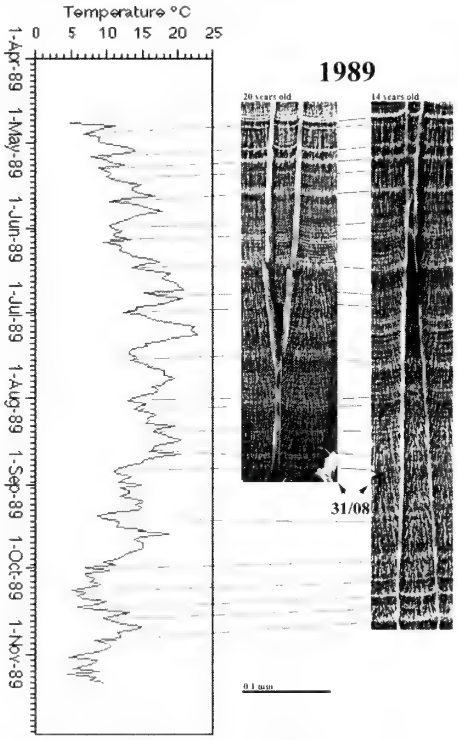

Fig. 11. Comparison between daily air temperatures and the microgrowth pattern in the annual growth increment of 1989 in two shells from the Vramsån River. Note that the strong differences in daily temperatures, not the actual temperatures, seem to produce the retardation zones.

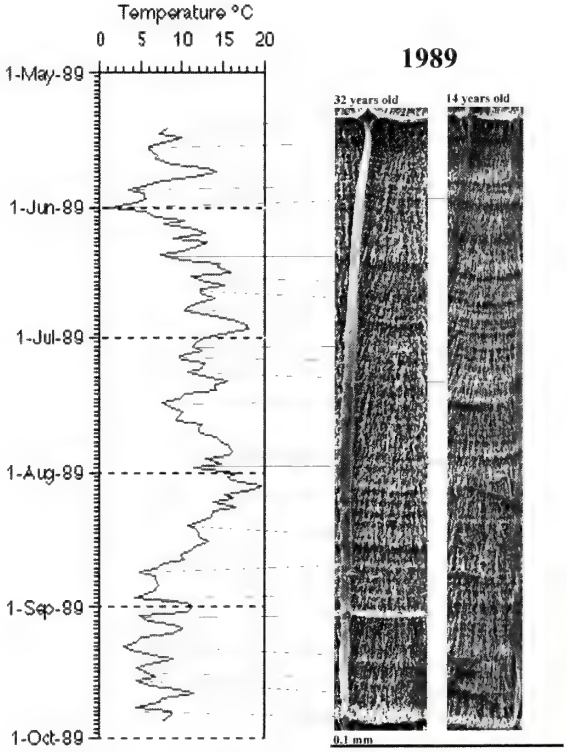

Fig. 12. Comparison between daily air temperatures and the microgrowth pattern in the annual growth increment of 1989 in two shells from the Välijoki River. Note that the strong differences in daily temperatures, not the actual temperatures, seem to produce the retardation zones.

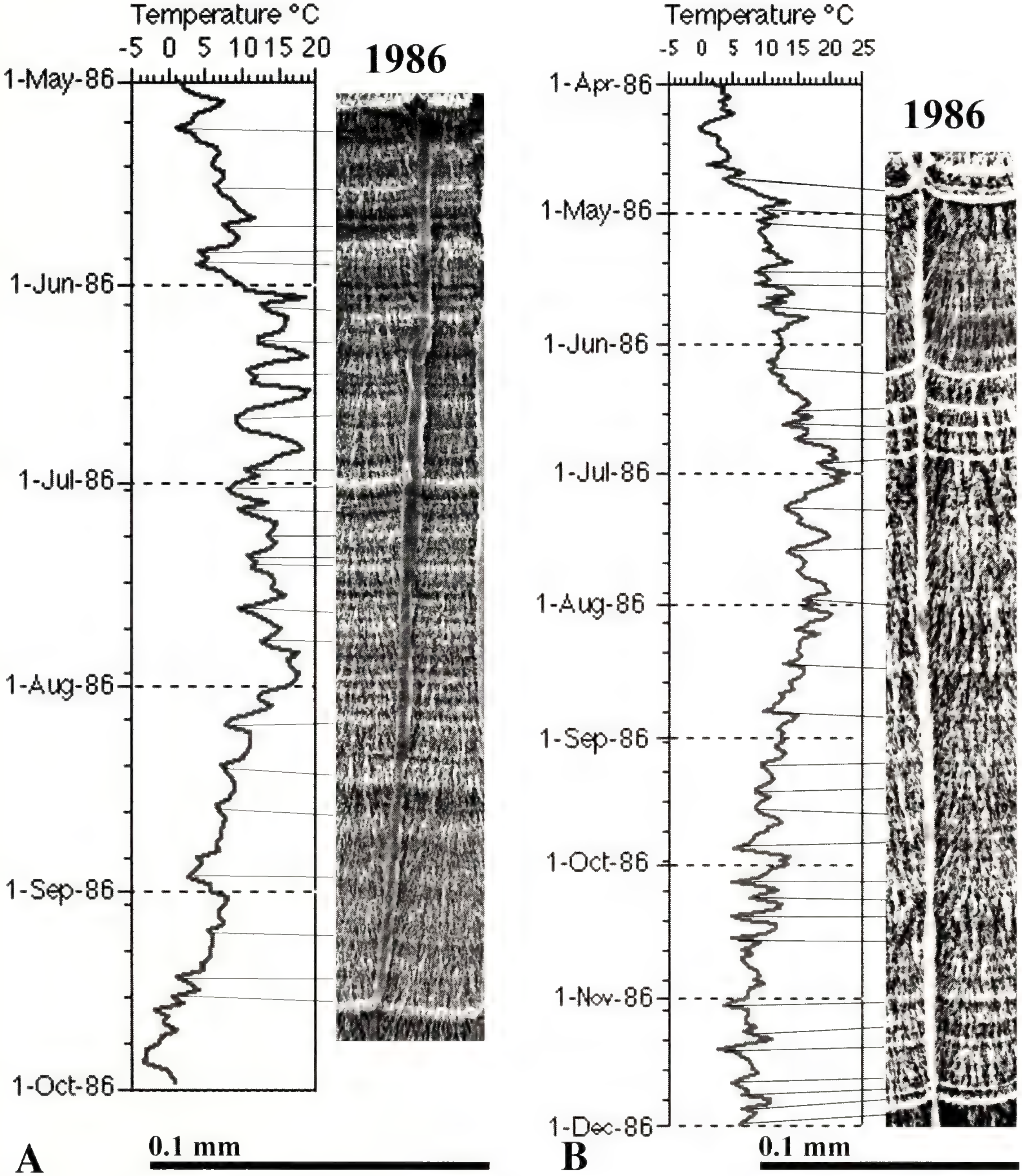

Fig. 13. A. Comparison between daily air temperatures and the microgrowth pattern in the annual growth increment of 1986 in a shell from the Välijoki River. Note that the growth season comprises 143 days (when the temperature is 5°C or higher) and the number of microlamellae is 148 with a counting error of ± 10. B. Comparison between daily air temperatures and the microgrowth pattern in the annual growth increment of 1986 in a shell from the Vramsån River. Note that the growth season comprises 219 days (when the temperature is 5°C or higher) and the number of microlamellae is 200 with a counting error of ± 30.

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The Geometry of Bivalve Shell Chemistry and Mantle Metabolism

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Abstract: Modern technology has arrived at a point where it can renew the revolution in understanding spatial relationships that occurred during the Renaissance. It was then that the discovery of geometric perspective made it possible to describe three-dimensional objects in nature with unprecedented detail. The discovery led to the development of modern science, and the moment at which the blue mussel, *Mytilus* sp., became an object of geometric curiosity is preserved in a remarkable illuminated manuscript, the *Mira Calligraphiae Monumenta.* Modern instrumentation has made it possible to enhance the classical descriptions of growth and form with information on spatial variations at the micro- and even nano-level in the chemistry and crystallography of the mollusc shell and in the metabolism of the mantle. Integration of this information will make it possible to use the mollusc shell as a proxy for molluscan physiology as much as it has been used as a proxy for the environment in the past.

Digital imaging of the outer shell layer of *Mytilus* sp. shows that magnesium (Mg) and sulfur (S) are concentrated along the margins of calcite prisms, but especially along the terminations of the crystals. The alignment of terminations of adjacent crystals thus produces compositional growth bands. These observations suggest that the organism actively uses Mg and S (as a component of the matrix) to control the elongation of the crystals in its shell, hence to determine shell form along different axes. Regions of the shell with high Mg and S levels appear to have been deposited by the mantle with a relatively high glucose metabolic activity, in contrast to shell with a high calcium (Ca) content. Stable carbon (C) isotope ratios in the calcite of *Mytilus* sp. shell (measured by other researchers), and nuclear magnetic resonance (NMR) spectroscopy of the mantle (reported here for the first time), offer independent support for the results of the glucose metabolic studies. Ultimately, it may be possible to develop a comprehensive model of molluscan shell growth and composition as a function of gradients in metabolism of the mantle.

Key Words: Bivalve, shell, chemistry, mantle, ATP

The purpose of this report is to suggest a link between the metabolism of the bivalve mantle and the chemistry of its shell. Traditionally, studies of molluscan shell chemistry have been limited to exploring connections with the environment (Rosenberg, 1980, 1990, for review). A dramatic example of recent work is Stanley and Hardie's (1998, 1999) suggestion that the composition and mineralogy of marine invertebrate skeletons over the course of geologic history have been a function of secular variations in the rate of seafloor spreading and consequent changes in the Mg/Ca ratio of seawater. The philosophy of the present report is that, as interesting as these environmental stories are, they are one-dimensional because they do not factor the organism's physiology into the equation. Careful analysis of such studies almost inevitably points to residuals in the data that environmental factors do not explain, and Stanley and Hardie (1998) themselves note that molluscs are one of the groups for which calcification is not strongly linked to seawater chemistry. Thus, molluscs are likely candidates for a model of shell micro-structure and composition in which physiology is at least as important a determinant as environment.

King Lear's fool asked him, "Canst tell how the [clam] makes his shell?" Lear replied that he could not, the fool responded that neither could he, and the King went on to a tragic end. It may be equally futile to hope for a comprehensive model that factors "absolutely everything" into the equation of shell growth and which will answer the question that Lear's fool asked any better than traditional approaches to shell chemistry have. But the search is a reaction to the "arrogance of the human mammal" who assumes that, on the one hand, the vertebrate skeleton is embedded in tissue and apparently sequestered from and independent of the environment. And on the other, that the chemistry of the bivalve shell is entirely explained by changes in the external milieu because the shell is separated from seawater by at best a thin film of periostracum. There must be more to the story than that.

The search for a "comprehensive" model is simply a reasoned conjecture that we have overlooked some exciting connections between molluscan shell chemistry and mantle physiology because we have blinded ourselves to them. A huge amount of substantive research has been done on molluscan physiology (*e. g.* Bayne and Newell, 1983; Hochachka, *et al.*, 1983; Storey and Storey, 1983; De Zwaan, 1983; Bishop *et al.*, 1983; Wheeler, 1992 for thorough discussions). But very little of that has ever been tied directly to molluscan shell chemistry, even though the paucity of such connections has been duly noted (Wilbur and Saleuddin, 1983).

MYTILUS AND THE REVOLUTION IN SPATIAL RELATIONSHIPS

Mytilus is the focus of this report because it is arguably one of malacology's best known genera-morphologically, mineralogically, genetically, and ecologically. At present it is not clear how all of these data sort at different taxonomic levels for, in 1992, Seed identified three distinct evolutionary assemblages, *M. edulis, M. galloprovincialis,* and *M. trossulus* on the basis of morphometric and allozyme information. Data obtained prior to 1992 (as well as that presented in this report for the first time) come from mussels identified by only a few morphological characters, and therefore identified with certainty to genus only. For the future, Seed's work affords the opportunity of testing the robustness and describing the systematic variation of any comprehensive model of growth on several closely related species.

The rationale of this report derives from the moment in Western cultural history when the ubiquitous mussel became an object of naturalistic curiosity. A sea change in the understanding of spatial relationships marked the moment and the Renaissance obsession with perspective generated it. The thesis of this paper is that modern instrumentation is on the verge of renewing that spatial revolution.

During the Middle Ages, animals and plants were depicted in illuminated manuscripts as flat and cartoon-like, often distorted and grotesque, confined to the margins of pages or imprisoned in spaces within letters. All of this reinforced the Church's teaching that Man was separated from nature (Camille, 1992; Kaufmann, 1993). However, the Renaissance discovery of perspective made it possible to depict objects in unprecedented three-dimensional detail, in other words to see animals and plants scientifically for the first time. Geometric perspective in particular made the formal studies of anatomy, biology, and optics possible (Edgerton, 1991), and also geology (Rosenberg and Kasl, 1996; Rosenberg, 1998). A most relevant example is D'Arcy Thompson's (1992 edition, originally published 1917), "On Growth and Form," in which Dürer's sixteenth century perspectival studies of animals and humans are used to show how apparently different body shapes are related to one another by variations in growth rate along selected geometric axes and, second, how those body plans are adapted to the environment ("form follows function"). The book led to modern studies of allometry (Gould, 1966, 1970), and these in turn inspire the spatial analyses of mussel shell composition and physiology in this report. One would expect that the composition of the skeleton and the physiology of its formation are as geometric as its morphological development, all progressing through life with interrelated spatial-temporal patterns.

The defining moment for *Mytilus* sp. came shortly after Dürer's work and is preserved on two pages of an illuminated manuscript known as the *Mira Calligraphiae Monumenta* (annotated by Vignau-Wilberg and Hendrix, 1992). The manuscript records a seminal moment in the transition between the flat and spiritual Medieval world and the three-dimensional and naturalistic modern world. Georg Bocskay, a scribe, wrote the manuscript in 1560 at the behest of the Habsburg emperor, Ferdinand I. The text in Fig. 1 is Saint Ambrose's commentary on Luke 19:29 in his Expositio evangelii secundum Lucam (E. Teviotdale, pers. comm.). Some 34 years later, Joris Hoefnagel, an illuminator, was commissioned by Rudolf II, Ferdinand's successor, to illustrate the volume and he drew the images of the mussel, the ladybird, and the flower on the page shown.

The technical issue of interest is the illusionistic, three-dimensional detail with which *Mytilus* sp. is illustrated. It may be the oldest scientific image of *Mytilus* sp. The interior of the mussel shell is clearly shown on the recto ("front"), as though it sits on top of the page (Fig. 1 left). It is indistinctly drawn on the verso ("back"), as though it is seen through the page (Fig. 1, right). Similarly, the ladybird and the flower.

The past is the key to future research on *Mytilus* sp. Technical developments of the past few decades promise to clarify the three-dimensional spatial variation in metabolism of the molluscan mantle and chemistry of the shell at ever diminishing scale as well as in ever increasing detail, just as the Renaissance spatial revolution did for morphology long ago. Nuclear magnetic resonance (NMR) now facilitates micro-physiological analyses. Modern, nondestructive techniques that do not require dissolution or ashing of the shell prior to analyses show special potential for studying shell characteristics because they facilitate simultaneous mapping of nano-structural as well as nano-compositional variations. These instruments include cathodoluminescence microscopy (Hawkes *et al.*, 1996; Barbin *et al.*, 1991), synchrotron x-ray fluorescence (Thorn *et al.*, 1995), proton-induced x-ray emission (Carriker *et al.*, 1991; Thorn *et al.*, 1995), atomic-force microscopy (Donachy *et al.*, 1992; Giles *et al.*, 1995; Sikes *et al.*, 1998), and electron probe microanalyses (Rosenberg and

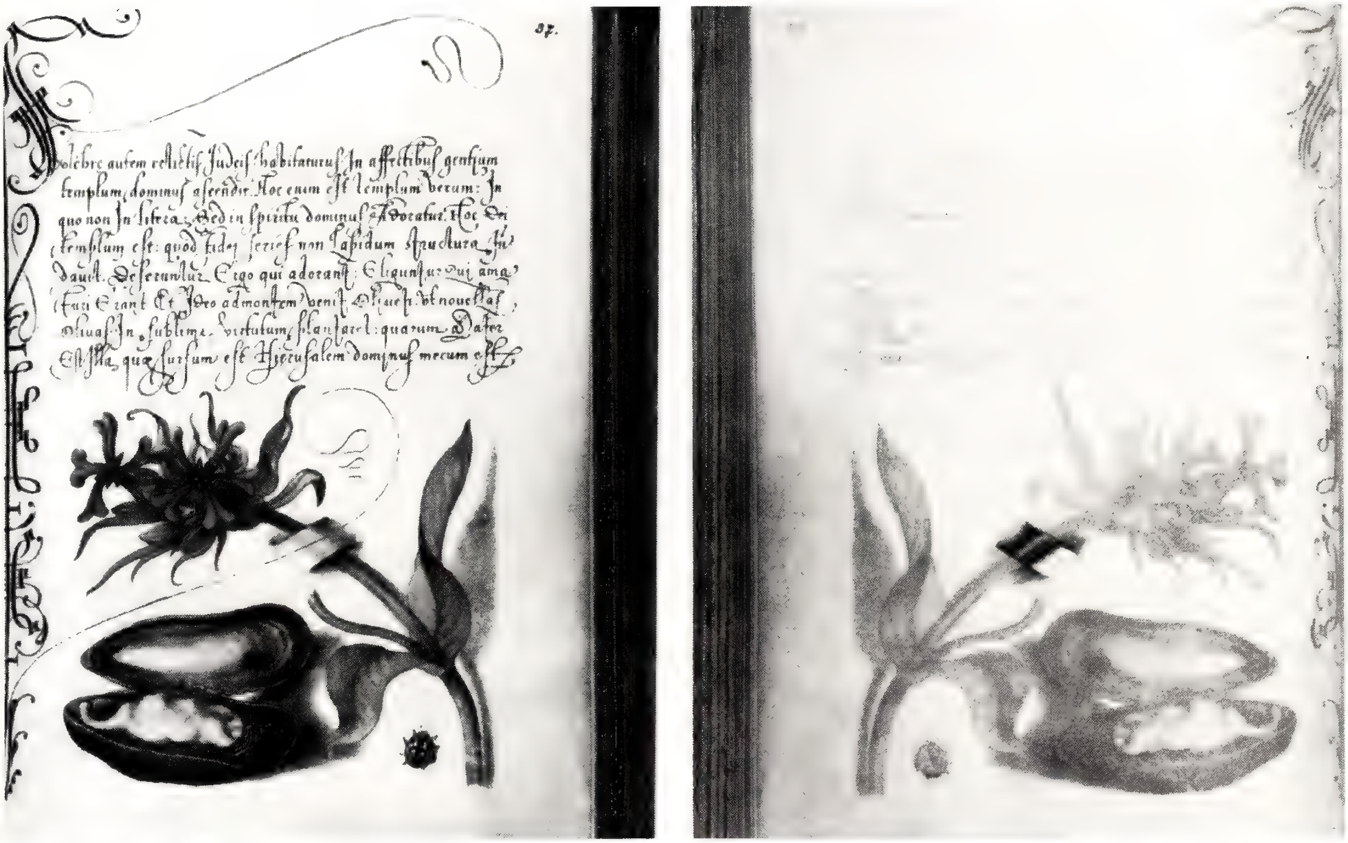

Fig. 1. Maltese Cross, European Edible Mussel, Fourteen- or Ten-Spot Ladybird. From *Mira Calligraphiae Monumenta*. Left, Folio 37, recto. Right, Folio 37 verso. Joris Hoefnagel (illuminator) and Georg Bocskay (scribe). Written 1561-1562, illuminated circa 1591-1596. Ink, watercolors, and gold and silver paint on parchment and paper bound between pasteboard, covered with red morocco. 6-9/16 x 4-7/8 in. With permission of the J. Paul Getty Museum, Los Angeles.

Hughes, 1991; Parker and Rosenberg, 1992; Rosenberg and Parker, 1992). Each has unique strengths and limitations, and the pictures emerging from them are adding a new dimension to the classical, systematic descriptions of morphology that have their roots in the early Renaissance.

Of all the elements studied by these techniques, magnesium (Mg) and sulfur (S) would seem to have the greatest potential as proxies for molluscan physiology (Rosenberg, 1980, 1990; Rosenberg and Hughes, 1991; Mann, 1992). Both Mg and S are involved at least indirectly in cellular energetics. As will be discussed below, Mg forms complexes with ADP and ATP and is also known to interfere with carbonate mineral crystallization. It is conceivable that S is present in trace amounts of mineral sulfates, but it is presumed to be concentrated primarily in acid mucopolysaccharides and amino acids within the shell matrix, which is metabolically far more costly to produce than the mineral fraction. Thus the concentration and distribution of both elements may testify to the metabolic activity of the mantle epithelium at the time and place where they were deposited in the shell.

MATERIALS AND METHODS

Mytilus sp.

The specimens of *Mytilus* sp. used for digital imaging of shell microstructure were obtained in July, 1988 and were living at mean sea level on rocks along Northwest Island, located a few hundred meters offshore of Walla Walla College Marine Lab, Anacortes, Washington, U. S. A. These are the same specimens whose physiology and shell composition were reported in Rosenberg and Hughes (1991), Rosenberg *et al.* (1989), and Rosenberg and Parker (1992). Although these specimens were living in an environment in which the average summer water temperature is approximately 12°C and in which average salinity is normal, it is likely that they were subjected to considerable ranges in both factors due to their emergence and submergence, and their repeated exposure to rainfall and variations in atmospheric temperature during tidal fluctuations. The specimens were mature (approximately 40 mm from umbo to the growing margin). The marginal portion of the outer shell layer was analyzed using digital electron probe microscopy (EPMA). This is the same portion of the shell secreted by strips of mantle tissue whose carbohydrate metabolism had been studied in vitro using C^{14} -glucose (Rosenberg *et al.*, 1989; Rosenberg and Hughes, 1991).

Nuclear magnetic resonance (NMR) studies of mantle physiology were undertaken on *Mytilus* sp. that were acquired chilled from the east coast by an Indianapolis fish market. These specimens were placed in artificial seawater that was oxygenated with a pump and air stone and kept at ambient temperature for 24 hours before sacrifice. A scalpel was used to sever the adductor muscle and strips of mantle were then excised for *in vitro* NMR analyses.

Digital Electron Probe Microscopy (EPMA)

The techniques of digital EPMA employed in mapping the distribution of elements such as Mg, S, Ca, and Na in the shell of *Mytilus* sp. have been described previously by Parker and Rosenberg (1992) and Rosenberg and Parker (1992) who reported for the first time that these elements constitute compositional growth bands comparable to structural growth increments that are evident in acetate peels or thin sections viewed in an optical microscope. These analyses were done on a Cameca EPMA at Pharmacia (Monsanto) Corporation, St. Louis, that had three wavelength dispersive spectrometers interfaced with a Kevex 8000 analyzer/imaging system. They have subsequently been repeated on two additional microprobes, a second Cameca courtesy of the Cameca Corporation at its headquarters in Paris, and a JEOL 8900 SEM/EPMA in Japan, courtesy the JEOL Corporation. Briefly, element maps were collected at 2000X, which enabled acquisition of 256 X 128 pixel arrays with a spatial resolution of ~ 0.25 µm, nearly an order of magnitude better than previous analyses of shell chemistry.

Nuclear Magnetic Resonance (NMR) Measurements

Nuclear Magnetic Resonance (NMR) studies of metabolic activity in the mantle of *Mytilus* sp. were undertaken to test the validity of metabolic studies that Rosenberg *et al.* (1989) previously obtained using C^{14}-labeled glucose. Rosenberg *et al.* found that the strip of mantle situated along the slow-growing lateral margin of the shell was actively metabolizing and apparently producing organic- and Mg-rich prismatic calcite and shell with a high curvature. In contrast, mantle that was metabolizing less actively at the point of maximal accretion produced prismatic calcite with less organic matter and less Mg, as well as a flat shell (Fig. 2, sections A vs D, respectively).

Biological phosphates, particularly the high-energy phosphate, adenosine triphosphate (ATP), its phosphotransfer product, adenosine diphosphate (ADP), and the guanido-phosphate energy store, phosphoarginine in the case of most invertebrates, give an indication of the energy state of cells and tissues. The only natural isotope of phosphorus, ^{31}P, has spin 1/2 and is, therefore, observable by NMR. Thus, ^{31}P NMR of a tissue sample can reflect the state of energy metabolism in that tissue.

^{31}P NMR measurements of marginal mantle strips were made at 121.4 MHz on a Varian UNITY-300 NMR spectrometer equipped with a high-stability variable temperature controller and a 10 mm broadband probe. Tissue samples were held against the wall of a 10 mm NMR tube by a coil of 1 mm o.d. polyethylene tubing through which aerated superfusion media was introduced into the bottom of the NMR tube by gravity flow from a reservoir outside the spectrometer. Superfusion fluid was actively pumped out of the NMR tube from about 1 cm above the top of the NMR spectrometer probe observe coil at 8 ml/min by a Buchler Instruments Polystaltic peristaltic pump. A glass capillary that contained 100 µl of 4 mM phenylphosphonate for the internal chemical shift reference at 13.0 ppm was inserted into the center of the coil in the NMR spectrometer tube. NMR spectral parameters were: sweep width, 5814 Hz; number of data points, 8192; number of transients 1024; recycle delay, 2 s; and line broadening, 20 Hz. All spectra were taken at 21°C and each spectrum required 46 minutes for acquisition.

RESULTS

Digital Electron Probe Microscopy (EPMA)

The Mg concentration in the outer calcitic shell of *Mytilus* sp. ranges up to approximately 0.50% by weight, and the S up to approximately 0.30% by weight. Mg/Ca and S/Ca ratios are respectively 1.25 and 1.40 times higher

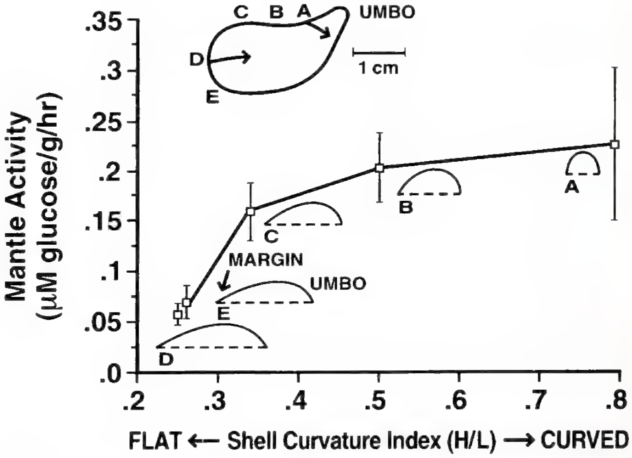

Fig. 2. Glucose metabolic activity (µM glucose/g/hr) in the mantle of *Mytilus* sp. at five intervals (A-E) long the margin vs. shell curvature measured from the margin towards the umbo. Standard error bars are shown for metabolic activity. Adapted from Rosenberg *et al.* (1989) and Rosenberg and Hughes (1991).

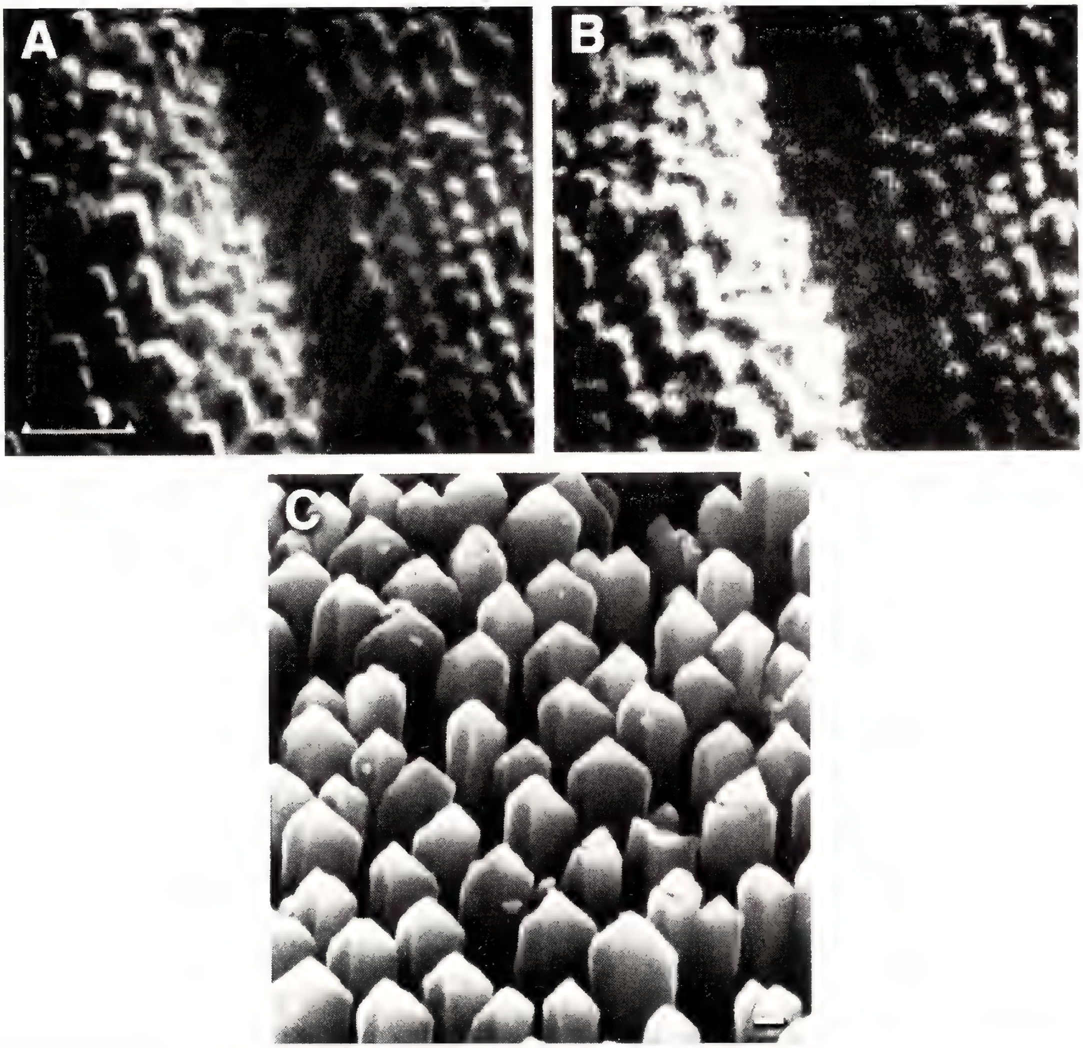

Fig. 3. A. Digitized x-ray micrograph of magnesium distribution in the outer shell layer of *Mytilus*. Chevron pattern of distribution of Mg indicates that the element is concentrated at the terminations of the calcite prisms (cf. Fig. 3C). Alignment of the termination produces compositional bands. Mg is weakly visible along the sides of the prisms. Scale = 10 µm. B. Digitized x-ray micrograph of sulfur distribution measured simultaneously with and at the same scale as Mg (Fig. 3A) in the outer shell layer of *Mytilus*. S is also concentrated at the terminations of the prisms, but extends farther from the tips than the Mg. C. SEM image of prismatic calcite in the outer shell layer of another *Mytilus*. Courtesy of Dr. Joseph Carter. Scale = 3 µm.

where growth is slow and curvature is high than along axes of rapid growth and low curvature (Area A vs D in Fig. 2, from Rosenberg and Hughes, 1991). Both elements constitute compositional growth bands (cf. Parker and Rosenberg, 1992), and Fig. 3 is an enlarged, or "zoom" image of Mg (Fig. 3A) and S (Fig. 3B) in a portion of one of them. Both Mg and S are concentrated about the terminations of the fibrous calcite prisms in chevron-shaped zones (cf. Fig 3C, which is an SEM image, courtesy of Joseph Carter, of the prisms in another *Mytilus* sp. shell). To a lesser extent the elements are also concentrated along the lengths of the prisms where they are weakly visible in Fig. 3A, B. The prism terminations, here pointing in the direction of growth, are aligned like the tips of stacked pencils, so the Mg and S capping them constitute compositional growth bands. Neither the Mg nor the S are uniformly distributed across a single band, implying that local conditions of concentration along a single contemporaneous growth surface vary, in spite of coordinated deposition. The Mg and S zones do not appear to conform perfectly (Fig. 3A, vs 3B); the S extends a bit farther from the crystal tips than does the Mg. This observation is supported by overlapping digital images of the two elements (color images not included here) and is not an artifact of instrument parallax; the displacement of the elements is not reversed when the detecting crystals on the instrument are exchanged in opposing spectrometers. However, it is not clear whether these spatial differences persist throughout the shell, and there is reason to believe that the relationship varies with the season of growth. Fritz *et al.* (1991) have found that the prismatic crystals shift their orientation relative to the inner surface of the shell throughout the year. Likewise, it is not clear whether the Mg and S are actually present in a pure "organic" phase (*i. e.* mineral-free, lacking Ca). Ca was analyzed simultaneously with Mg and S, and it is ubiquitous at all positions, albeit in reduced concentrations where the level of trace elements is high. Analyses of shell cleaned with sodium hypochlorite (bleach) have been undertaken in order to determine whether Mg- and S-enriched caps can be detected even if the organic matrix has been removed but results are presently inconclusive and this question merits serious future study.

Nuclear Magnetic Resonance (NMR) Measurements

NMR spectra obtained from analysis of *Mytilus* sp. mantle are shown in Fig. 4. Three peaks are labeled: the phenylphosphonate standard, phosphoarginine, and β–ATP (beta phosphate signal from nucleotide triphosphates, predominantly ATP). The ratios of the peak areas of both phosphoarginine and β-ATP to that of the standard are at least 20% higher in area A than D. (This value is conservative, as differences in a second analysis exceeded 100%.) The two large unlabeled peaks between the phosphoarginine and β-ATP peaks arise from nucleotide triphosphates and nucleotide diphosphates, predominantly ATP and ADP. The ratios of these two peaks to the standard compared with the β-ATP peak to the standard indicate that area A has very little nucleotide diphosphate (predominantly ADP), in contrast to area D.

Phosphoarginine is the high-energy phosphate compound that invertebrates use to store energy and is the source of the high energy organic phosphate catalytically transferred to ADP to replenish ATP rapidly in the early stages of high energy demand (Lehninger, 1982). Phosphocreatine performs this function in vertebrates. ATP is catalytically converted to ADP with transfer of the high energy terminal phosphate to a receiver molecule as energy is utilized. Thus, the spectral differences noted above indicate that mantle from area A has a greater degree of high energy phosphate availability than mantle from area D. This suggests that mantle from area A has a capacity for greater metabolic activity than mantle from area D. Although the data do not assess non-phosphate metabolism of carbon or nitrogen *per se*, reductions and oxidations will be greatly slowed in the absence of adequate ATP.

Finally, the position of the β-ATP peak on both spectra to the left of –20 ppm indicates that it is saturated with Mg in both area A and area D (Vasavada *et al.*, 1984). Consequently, the ADP is also saturated with Mg.

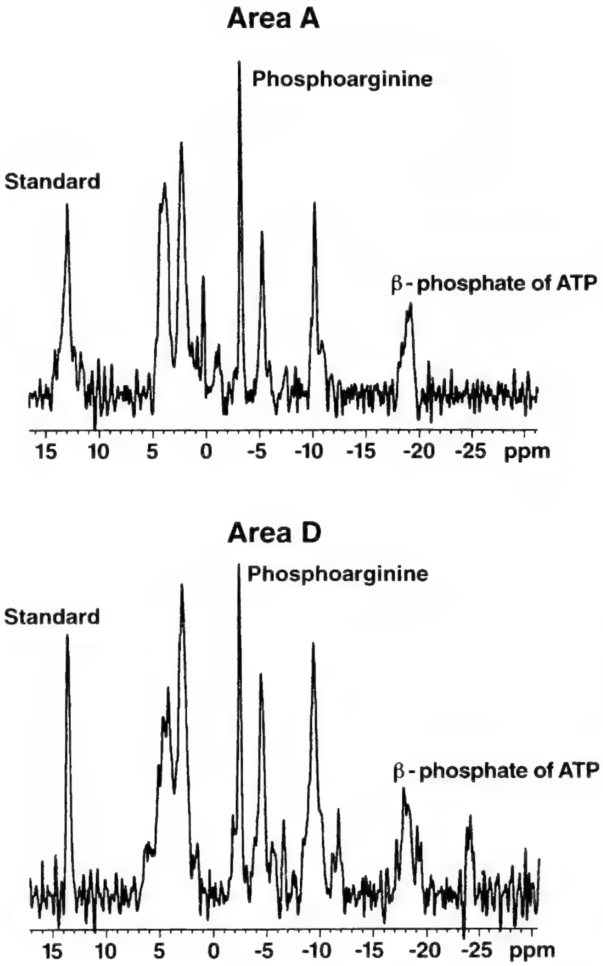

Fig. 4. NMR spectra of ^{31}P in marginal mantle of *Mytilus* sp. Scaled intensity of peaks (Fast Fourier Transform) on the ordinate vs. chemical shift (resonance frequency in Hz divided by observation frequency in MHz, hence units = ppm) on the abscissa with increasing negativity to the right by convention. The standard is referenced against 85% phosphoric acid at 0 ppm, hence the chemical shift can be positive or negative. Top: analysis of mantle from margin at A in Fig. 2 (along slow-growing lateral axis, shell with high curvature and having a prismatic calcite layer with relatively high organic (S/Ca) and Mg/Ca content, deposited by mantle having relatively high glucose metabolic activity). Bottom: analysis of mantle from margin at area D in Fig. 2 (along axis of maximum growth, flat profile, and having prismatic calcite with relatively low organic (S/Ca) and Mg/Ca content, deposited by mantle having relatively low glucose metabolic activity). Peaks representing phosphoarginine and β-ATP (beta phosphate signal from nucleotide triphosphates, predominantly ATP) are approximately 20% higher relative to the phenylphosphonate standard in mantle from area A than D. Mantle from area A thus has a greater degree of high energy phosphate availability than mantle area from area D. Peak position of β-ATP to left of –20 ppm indicates that both ATP and ADP are saturated with Mg.

DISCUSSION: METABOLIC MODELS FOR MOLLUSCAN SHELL GROWTH

The data presented here support the existence of metabolic gradients across the mantle of *Mytilus* sp. and thus encourage continued pursuit of a generalized model of shell growth in which those gradients determine both shell form and composition. Trace elements such as Mg and S (an index of various organic components) are concentrated at the terminations and along the sides of prismatic shell crystals suggesting that they are actively involved in regulating rate and orientation of crystal growth, and thus shell shape. The presence of compositional growth bands indicates that energy use fluctuates cyclically. More energy is required when and where Mg and S are concentrated, especially areas of the shell that grow slowly and have high curvature.

In 1989, Rosenberg *et al.* determined that the rate of glucose metabolism in the strip of mantle along the margin of the shell of *Mytilus* sp. is least at the axis of maximum growth and greatest at the axis of slowest growth (Fig. 2, area D vs A, respectively). The rate of glucose metabolism was lower within the "inner mantle," a strip of tissue a few millimeters wide adjacent and just interior to the margin, and there were no significant differences in the rate anywhere along its extent. This means that the metabolic gradient from the margin of the mantle towards the umbo is steepest along the axis of slowest growth (Fig. 2, area A).

Rosenberg and Hughes (1991) developed a geometric model of growth in which the metabolic gradient of the mantle produced a proportional value of shell inflation and thus determined shell shape along any axis. Sections of the shell that have a high curvature have a small radius, and sections of the shell that are flat are extended. Both geometries augment surface area to volume ratios, hence optimize diffusion of oxygen and dissolved nutrients and wastes. Inversely, spherical shells with a large diameter would have a small surface area to volume ratio. This would explain why enormous spherical bivalves are not common (the genus *Tridacna* could be the closest exception but its mantle extends beyond its gape and it has exploited symbiotic zooxanthellae to enhance its respiration). It also explains why populations of flat bivalves are typical of dysaerobic facies, or anaerobic environments (Kauffman, 1988; Rosenberg *et al.*, 1989). However, it is not meant to suggest that a compressed morphology is not adaptive in oxygenated waters, and there are any number of families such as the Anomiids and Pandorids with compressed species that do reside in those habitats (R. Prezant, pers. comm.).

The "metabolic gradient" model is consistent with Michaelis-Menten theory of enzyme activity, which recognizes that either enzymes (catalysts) or substrate (fuel) limit the rate of metabolic activity, depending upon their relative concentrations (Lehninger, 1982). And it suggests a scenario in which enzymes or substrate diffuse from the site of generation or acquisition across the mantle, diminishing in concentration with distance and thus area covered. The problem is that the hypothesis is counterintuitive; one would expect metabolism to be greatest where growth rate is greatest. With this in mind, one would expect the alternative hypothesis, that orientation of the mantle determines shell shape (Huxley, 1932), to be more compelling. On the other hand, no one has ever tested Huxley's explanation nor has the question of physiological regulation of shell shape *per se* received attention in modern scientific study. Raup and Michelson (1965) and Raup (1966) describe molluscan shell form as a function of combinations of coiling parameters whose realization in nature depends on maintenance of surface area to volume relationships, but it does not attempt to explain how those parameters are determined physiologically. In any event, the "metabolic gradient" model does argue for factoring the relative efficiency of deposition of shell of various compositions into any model of shell growth. And recent studies of mussel metabolism underscore the issue; faster-growing individuals have lower maintenance metabolisms because gross metabolic efficiency appears to be a function of reduced turnover of tissue protein relative to energy absorption (Hawkins and Bayne, 1991).

Rosenberg and Hughes (1991) reasoned that their metabolic gradient model would be more credible if they could demonstrate that their data were consistent with Palmer's (1981, 1983) hypothesis of the evolutionary advantage of mineral- vs organic-rich shell. Palmer discussed evidence showing that natural selection has favored mineral-rich over organic-rich shell during the course of evolution. Organic-rich shell is more expensive to produce than mineral-rich shell. For an introduction to the energetics of elaboration of the organic fraction vs the mineral phase, see Wilbur and Saleuddin (1983). Briefly, it takes four ATP molecules to assemble each of the many peptide bonds (short amino acid sequences) in shell protein. It takes but one ATP molecule to transport two Ca^{+2} ions through mitochondria, and although there is an additional cost to transport any HCO_3^{-1} (bicarbonate ion) that becomes shell carbonate, the cost of the protein elaboration greatly exceeds the sum of the two.

If Palmer's hypothesis is correct, one would expect that organic-rich shell within the same individual, as well as among different species, would be metabolically more expensive to produce than mineral-rich shell. This is of course a reasonable assumption to apply to bivalves that have an outer layer of prismatic calcite, and an inner layer of nacreous or foliated aragonite; prismatic calcite typically has a higher content of organic matrix than aragonite (Sikes *et al.*, 1998), and, as stated above, Rosenberg and Hughes (1991) have shown this for *Mytilus* sp. in particular. Rosenberg and Hughes (1991) also tested the predicted correlation within several areas of the prismatic shell that differ in composition. They found (electron probe microanalyses) that the S/Ca ratio was highest in the prismatic shell that was deposited by the most rapidly metabolizing mantle, at the axis of least growth and highest curvature (area A in Fig. 2). Although some S could be present as SO_4^{-2} within the crystal lattice, S is most likely concentrated in the organic phase of the shell (as sulfated polysaccharides (Crenshaw and Ristedt, 1976), proteoglycans (Wada, 1980), or in certain amino acids themselves) and is thus a proxy for organic content.

Klein *et al.* (1996b) found that the $\delta^{13}C$ ratio in the calcitic shell layer of *Mytilus* sp. was highest at the ventral margin near the axis of maximum growth, and that it decreased towards the lateral margins where growth was slowest. Because organisms preferentially metabolize the lighter of two C isotopes (C^{12} vs. C^{13}), they concluded that the low value at the lateral margin indicates a high volume of metabolically derived C in the extrapallial fluid at that position. They also found that the ratio of Sr (strontium) to Ca in the calcitic shell decreased from the ventral to the lateral margin, which they reasoned was due to an increase in intracellular transport and Ca-pumping in the same direction.

Klein *et al.*'s (1996b) data are important not simply because they independently corroborate Rosenberg *et al.*'s (1989) determinations. They also help estimate the proportion of metabolic energy devoted specifically to shell formation. Rosenberg *et al.*'s studies were of glucose metabolic activity in *whole* mantle; the mantle is composed not only of epithelial cells responsible for secreting shell, but also of muscle, connective tissue, etc., which play no known role in biomineralization. While the cost of total protein synthesis in mussels likely accounts for a large fraction of total energy requirements (Hawkins and Bayne, 1991), and one would assume that the amount of energy devoted to shell formation would increase with total energy output, Klein *et al.*'s (1996b) data actually measure the production of C that is destined for the shell.

It would be worthwhile to factor the organic/mineral ratio into its components. The organic material in the shell consists of numerous constituents that variously inhibit and facilitate crystal nucleation, rate, and direction of growth. The long history of identification of these components and elaboration of their functions will not be reviewed here except to say that there is undoubtedly a metabolic cost associated with each. Borbas *et al.* (1991) have found that the phosphate content of soluble matrix isolated from *Mytilus* sp. shell is low (0.93 and 1.36% by weight of the soluble matrix in the calcitic vs. aragonitic layer, respectively). However, the total phosphate within the latter is "diluted" by virtue of the fact that there is less total organic matrix within it. Thus, the regulation of metabolic expenditures is parsimonious; the same constituents are involved throughout the shell, but their proportions differ.

The need to expend energy to maximize surface area along all axes of growth in order to facilitate diffusion across the mantle is consistent with the role that Mg is postulated to play in crystallization and shell growth. Mg^{+2} has long been known to act as a crystal poison that retards the growth of calcite and hydroxyapatite biominerals (Kitano *et al.*, 1969; Wilbur and Bernhardt, 1984), and of sedimentary calcites (Folk, 1974) because it substitutes for the larger Ca^{+2} ion in the crystal lattice, and distorts the unit cell. Active retardation of growth along short axes of high curvature would maintain a high surface area to volume ratio (volume increases with the cube of a sphere's radius, whereas surface area increases with the square). Furthermore, directed substitution of Mg^{+2} into the lattice alters the growth rate along the a- relative to the c- crystallographic axis, and thus could influence crystal shape (Folk, 1974; O'Neill, 1981), orientation at the surface of the shell (seasonal variations observed by Fritz *et al.*, 1991 and discussed above), and the crystallographic forms of prism terminations, whose diversity has yet to be explained (J. Carter, pers. comm.).

It is assumed here that Mg^{+2} ions are actively transported to the growing crystal surfaces, particularly the terminations, where they influence crystal growth rates as described above. But, it should be emphasized that Mg is probably not confined to the interior of the calcite lattice and that its function may be localized at the surface of growing crystals. The digital images of Mg and S distribution in *Mytilus* sp. (Fig. 3) provide evidence that Mg is intimately, but not exclusively, associated with the sulfur-containing fraction, for the Mg and S concentrations overlap but do not perfectly conform. In other mollusks, the sulfur-containing fraction of the shell has been found to constitute proteoglycans and polysaccharides that are especially enriched in nucleating crystals (Wada, 1980 and Crenshaw and Ristedt, 1976). Although it is generally presumed that organic molecules control the spatial distribution, orientation, and rate of nucleating minerals (*i. e.* matrices are templates for biominerals), it is unknown whether the presence of S *per se* facilitates, retards, or has no effect on biomineralization or Mg deposition. The question how Mg^{+2} interacts with different organic compounds to influence mineral and matrix deposition is also unresolved, despite Kitano *et al.*'s (1969) *in vitro* path finding studies.

Klein *et al.* (1996a,b) reported that values of Mg/Ca in the prismatic shell of *Mytilus* sp. vary with temperature, and that there is no relationship between Mg/Ca and Sr/Ca ratios in the same shells. Given Klein *et al.*'s (1996a) observation that the Sr/Ca ratio in prismatic shell increases towards the ventral margin, the lack of correlation with Mg/Ca would seem to conflict with Rosenberg and Hughes' (1991) data that show that the value of Mg/Ca is highest at the lateral margin. However, it is not clear whether Klein *et al.* (1996b) measured Mg/Ca ratios across the entire shell or confined their sampling to the portion along the axis of maximum growth. The focus of their study was the axis of maximum growth along which $\delta^{13}C$ ratios suggested that mineralization is in near-equilibrium with seawater. The strong correlation between the Mg/Ca value and ambient temperature along that axis is consistent with that finding. However, they used inductively-coupled-plasma-atomic-emission spectroscopy (ICP-AES), which requires separation and removal of the organic fraction by ashing prior to analysis. They assumed that Mg is bound entirely to carbonate within the mineral fraction of the shell. The observation reported here that Mg and S are concentrated at the terminations of the calcite prisms suggests that the assumption is not warranted, and that Mg may be present in both phases of the shell, if not entirely restricted to the organic fraction. Thus it is possible that some Mg was lost from ICP analysis and/or calculations of weight percent Mg were skewed due to its association with the organic fraction.

Mg^{+2} is essential for the enzymatic utilization of both ADP and ATP, yet its role in kinase reactions remains unknown despite intensive study (Vasavada *et al.*, 1984; Nageswara Rao, 1979; Nageswara Rao, pers. comm.). As stated above, our results show that both ADP and ATP are saturated with Mg^{+2} even though Mg^{+2} binds 10 times more strongly to ATP than to ADP and the affinity to both increases with pH (Lehninger, 1982). Mg increments within the shell are thus not likely to be a proxy of changes in either ADP or ATP saturation, but they could reflect competition between Mg^{+2} and Ca^{+2} for sites on calcium-binding proteins. Carbohydrate-complexed, calcium-binding proteins are known to occur in the molluscan mantle (Dogterom and Doderer, 1981), and they are likely to be involved in transport of Ca^{+2} from the mantle to the shell (Wilbur and Saleuddin, 1983). Mg^{+2} and Ca^{+2} compete for some of the same binding sites in calcium-binding proteins such as calmodulin, but NMR studies suggest that the occupation of those sites differs between the resting and stimulated state of the cell (Tsai *et al.*, 1987). Mg^{+2} also potentiates important enzymes, and Ca^{+2} competes for coordination sites on them. There is thus selective pressure for sequestering Ca^{+2} within the shell (Kretsinger, 1977; Lowenstam and Margulis, 1980). Mg growth increments within the shell thus may indicate the state of mantle cell activity, specifically the elaboration of Ca-binding proteins or enzyme activity.

CONCLUSIONS

If only King Lear had realized that the geometry of the bivalve shell holds clues to the answer of his fool's question, "Canst tell how the [clam] makes its shell?" If only he had had the means to observe the micro-structure and micro-chemistry of the shell, and to study micro-spatial variations in mantle physiology, he might have been able to construct a three-dimensional model of shell growth and form. No, make that four-dimensional, for growth and form change through geologic history. Surely, then, Lear's fate would have been far different. He would have had something to live for long after he lost his kingdom, and he could have spent the rest of his days in bliss, piecing together the puzzle of bivalve shell growth and recording his sense of wonder about it all for future generations. We owe Eleanor Clark (1966), author of, "The Oysters of Locmariaquer," for finding in Shakespeare's *King Lear* an old intellectual saw and applying it with such wisdom to malacology. Questions about nature are never final, they simply lead to more questions, and it is this mystery that propels our search for new knowledge. True, we will never know everything about how the bivalve grows its shell. But it's a good bet that the manifold data on shell chemistry and mantle metabolism will be less meaningful if they remain isolated fragments than if they are integrated within the holistic, geometric model of growth and form that had its origin long ago in the Renaissance, a model that has since proven so useful in understanding molluscan evolution.

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68th ANNUAL MEETING
THE AMERICAN MALACOLOGICAL SOCIETY
CHARLESTON, SOUTH CAROLINA
AUGUST 3 - 7, 2002

The 2002 American Malacological Society meeting will be held at the College of Charleston's Lightsey Conference Center in historic Charleston, South Carolina. The city is America's most beautifully preserved architectural treasure, featuring historic homes, restaurants, shops, museums, and tours. The Lightsey Center is a modern facility with a complete range of conference services.

Symposium: The Biology and Conservation of Freshwater Gastropods. The North American fauna includes about 500 nominal species of freshwater gastropods. But the taxonomy of many groups predates the modern synthesis, and great confusion exists regarding the specific identity of even the most common populations. As a consequence, large regions of the continent have never been adequately surveyed, and fundamental aspects of the ecology of many freshwater gastropod groups remain obscure. Absent a recommitment to basic research on the biology of freshwater gastropods, a critical element of our biota is in danger of slipping away. Organizer: Rob Dillon.

Other special sessions are in the planning stages. In addition, there will be general sessions for contributed papers on a wide variety of topics, in both oral and poster format. Several awards for student presentations will be given.

Housing will be available at modest cost in dormitory facilities at the College of Charleston. Lodging is also available at the Westin Francis Marion Hotel, located adjacent to the Lightsey Center.

A variety of special activities are planned, including evening programs, an expanded endowment auction, and a dinner cruise on Charleston Harbor. Field trips will be available for every taste, featuring both historic tours and a boat trip to pristine Bull Island.

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Hillis, D. M. 1989. Genetic consequences of partial self fertilization on populations of *Liguus fasciatus* (Mollusca: Pulmonata: Bulimulidae). *American Malacological Bulletin* 7(1):7-12.

Seed, R. 1980. Shell growth and form in the Bivalvia. *In: Skeletal Growth of Aquatic Organisms,* D. C. Rhoads and R. A. Lutz, eds. pp. 23-67. Plenum Press, New York.

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EDITORIAL COMMENT

This issue of the *American Malacological Bulletin* marks a major change in editorial staff. From its origin under the leadership of Robert Prezant (Editor-in-Chief 1983-1993) and through the succession of editors Ronald Toll (Managing Editor 1986-1993 and Editor-in-Chief 1993-2001), Paula Mikkelsen (Managing Editor 1994-1998) and Timothy Pearce (Managing Editor 1999- 2001) the journal has grown in scope and distribution. I appreciate the confidence and trust the members of the American Malacological Society have shown in me in offering me this position. I am grateful for all of the advice, cooperation, and leadership Ron and Tim have provided during the transition in editorship. I am especially pleased that Ángel Valdés has agreed to serve as Managing Editor of the journal. We have worked together to streamline the editorial process, making as much correspondence as possible electronic, and maintaining close communication despite large distances.

Janice Voltzow
September 2002

The unionid (Bivalvia) fauna of the Sipsey River in northwestern Alabama, an aquatic hotspot

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Abstract: Recent surveys for unionid bivalves were conducted in the mainstem of the Sipsey River and headwater tributaries (Tombigbee River drainage) during the summer and autumn of 1996-1999. A total of 35 species and 22 genera were found. Museum records from the upper Sipsey, based largely on the efforts of H. H. Smith during 1910-11, raised the total number of recorded unionids in the Sipsey to 42. Smith documented 25 species in the river; however, most of his collections were made in the mid- to upper-Sipsey, which has lower diversity. The three most common recently observed species in descending order of abundance were *Quadrula asperata* (I. Lea, 1861), *Pleurobema decisum* (I. Lea, 1831), and *Tritogonia verrucosa* (Rafinesque, 1820). Federally listed species observed recently include *Lampsilis perovalis* (Conrad, 1834) (threatened), *Medionidus acutissimus* (I. Lea, 1831) (threatened), *P. decisum* (endangered), *P. perovatum* (Conrad, 1834) (endangered), and *Potamilus inflatus* (I. Lea, 1831) (threatened). Species not observed recently but recorded in prior surveys include *Anodontoides radiatus* (Conrad, 1834), *Arcidens confragosus* (Say, 1829), *Plectomerus dombeyanus* (Valenciennes, 1827), *Q. metanevra* (Rafinesque, 1820), *Q. stapes* (I. Lea, 1831) (federally endangered), *P. taitianum* (I. Lea, 1834) (federally endangered), and *Toxolasma parvus* (Barnes, 1823). Many species are known recently or historically by only five or fewer recorded specimens including: *A. radiatus, Elliptio arctata* (Conrad, 1834), *Ligumia recta* (Lamarck, 1819), *P. taitianum, P. inflatus, Q. aspera* (Lea, 1831), *Q. metanevra, Q. stapes, T. parvus, Truncilla donaciformis* (I. Lea, 1828), *Uniomerus tetralasmus* (Say, 1831), *Utterbackia imbecillis* (Say, 1829), *A. confragosus,* and *P. dombeyanus*.

Unlike the mussel fauna of most Alabama streams, that of the Sipsey River is still relatively intact in terms of species richness despite impacts from mining, silvicultural, and agricultural activities. A concerted effort should be made to provide guidelines to manage floodplain and watershed activities to avoid future adverse impacts on this aquatic hotspot.

Key Words: Unionidae, freshwater mussels, bivalves, Sipsey River, Mobile drainage basin, Alabama

The southeastern United States harbors the richest freshwater unionid bivalve assemblage in the world (Bogan 1993a; Lydeard and Mayden, 1995; Neves *et al.*, 1997). The greatest diversity of unionids can be found in the Tennessee, Mobile, and Ohio drainage basins (Neves *et al.*, 1997). There are three major watersheds in Alabama (*i. e.*, Mobile, Tennessee, and Apalachicola) and several smaller eastern Gulf of Mexico streams, which serve as home to 177 recognized species and subspecies (Lydeard and Mayden, 1995; Lydeard *et al.*, 1999). Alabama ranks first in the number of unionid taxa in the United States with 60% of 297 recognized species (Lydeard and Mayden, 1995; Neves *et al.*, 1997), Tennessee (128 spp.) is second (Parmalee and Bogan, 1998), and Kentucky (103 spp.) is third (Neves *et al.*, 1997). Alabama owes its biological diversity to the presence of three major and several smaller river basins within its borders, the variety of physiographic regions and habitats the drainages traverse, and the antiquity and complex geology of the larger watersheds allowing for ample time and opportunity for speciation.

Unionids are one of the most endangered groups of animals in the world, with 70% of the species considered imperiled (*i. e.*, formally listed species via the Endangered Species Act or informally considered threatened or endangered) (Williams *et al.*, 1993; Neves *et al.*, 1997; Master *et al.*, 1998). Factors contributing to the decline of unionids include pollution, siltation due to poor land-use practices, impact from exotic species, and habitat modification and destruction especially from impoundments (see review in Neves *et al.*, 1997). Most of the major river systems in Alabama have been impounded including the Coosa, Tallapoosa, Black Warrior, Tennessee, and most recently the Tombigbee. The Tombigbee River has been impounded since 1976 when the "Tennessee-Tombigbee Waterway" was completed, converting the formerly free-flowing river into a series of reservoirs separated from each other by locks-and-dams (Williams *et al.*, 1992). Impoundments have eliminated and/or drastically modified vital habitat resulting in the loss of many unionid species (Williams *et al.*, 1992; Bogan *et al.*, 1995; Lydeard and Mayden, 1995; Neves *et al.*, 1997). The rich fauna of the Muscle Shoals of the Tennessee River in Alabama that was documented by Ortmann (1925) as the "richest fauna in the world" was halved from 79 species to 39 species (Garner and McGregor, 2000) and the species composition was altered dramatically and now includes largely reservoir-tolerant species (Ahlstedt and McDonough, 1993). Aside from extinction, impoundments have resulted in the extirpation of many species and the reduction of their formerly widespread distributions. For example, impounded waters upstream from the John Hollis Bankhead Lock and Dam of the Black Warrior River completely flooded an area formerly known as Squaw Shoals, resulting in the extirpation of 30 freshwater bivalve species (JDW, unpubl. data).

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Free-flowing rivers are a rarity in the nation (Benke, 1990) and represent important biological resources worthy of protection from further degradation. The last remaining free-flowing rivers of Alabama include the Locust Fork and Mulberry Fork of the Black Warrior River, the Sipsey River of the Tombigbee drainage, and the Choctawhatchee and Yellow rivers of the eastern Gulf region. The Locust and Mulberry forks and Sipsey River are part of the Mobile River drainage basin, which was recognized as one of the top 200 ecoregions in the world by the World Wildlife Fund (Olson and Dinerstein, 1998; Abell *et al.*, 2000). The Cahaba River is biotically diverse, though heavily impacted by wastewater treatment effluent. It is often considered free-flowing by some though it does have a small impoundment, Lake Purdy, on the upper reaches of the Little Cahaba River (Shepard *et al.*, 1997) and the lower ca. 50 kilometers (km) are influenced by the impoundment of the Alabama River.

The Locust Fork, Mulberry Fork, and Cahaba River have lost most of their unionid fauna from poor land-use practices including agricultural and industrial activities and urban and suburban sprawl (see Shepard *et al.*, 1997 for review). The Choctawhatchee and Yellow river systems still possess a diverse and abundant unionid fauna based on recent collections (SWM, JDW, Holly Blalock-Herod, unpubl. data). The Sipsey River is still believed to possess much of its historic unionid fauna. Although several unpublished documents and government reports have been written on the unionids of the Sipsey River, no comprehensive survey and summary of the historic fauna has been published.

The objective of this study was to examine the unionid fauna of the Sipsey River using museum records and recent collection efforts. The use of museum records provides an important and critical historical reference for more recent surveys and an opportunity to note any major qualitative changes in the fauna over time.

While the mussel fauna of the Sipsey River has been only sporadically collected over the years, the Tombigbee River has been the subject of several papers during the past century. Hinkley (1906) reported 40 species from the Tombigbee River system. In a more detailed account van der Schalie (1939) provided a review of the mussels in the main channel of the Tombigbee and described a new species, *Medionidus mcglameriae* van der Schalie, 1939. Williams *et al.* (1992) reported on the impacts of impoundments on the mussel fauna in the main channel of the Tombigbee downstream from the mouth of the Sipsey River. Williams (1982) provided distribution and habitat information for five of the endemic mussels that occur in the Tombigbee drainage, which were subsequently federally listed as threatened or endangered. The U. S. Fish and Wildlife Service (USFWS) has recently released the Recovery Plan for the Mobile River basin aquatic ecosystem (USFWS, 2000).

THE STUDY AREA

The Sipsey River is a tributary of the upper Tombigbee and drains an area of 2,044 km^2 (McGregor and O'Neil, 1992). Its headwaters originate in the Cumberland Plateau physiographic section of the Appalachian Plateaus province above the Fall Line (Sapp and Emplaincourt, 1975) in Marion County (Fig. 1) at an elevation of about 210 m above mean sea level (msl). The confluence of these headwater streams, the New and the Little New rivers, forms the Sipsey River just south of the Marion/Fayette county line. The Sipsey then flows south and southwest for about 184 km (115 river miles) through the East Gulf Coastal Plain physiographic section in Fayette, Tuscaloosa, Pickens, and Greene counties to its confluence with the Tombigbee River at river km 451.2 (river mile 282) at an elevation of about 34 m above msl (Fig. 1). Its drainage basin is unusual in being long and narrow with relatively few tributaries. Its lowermost reach forms the

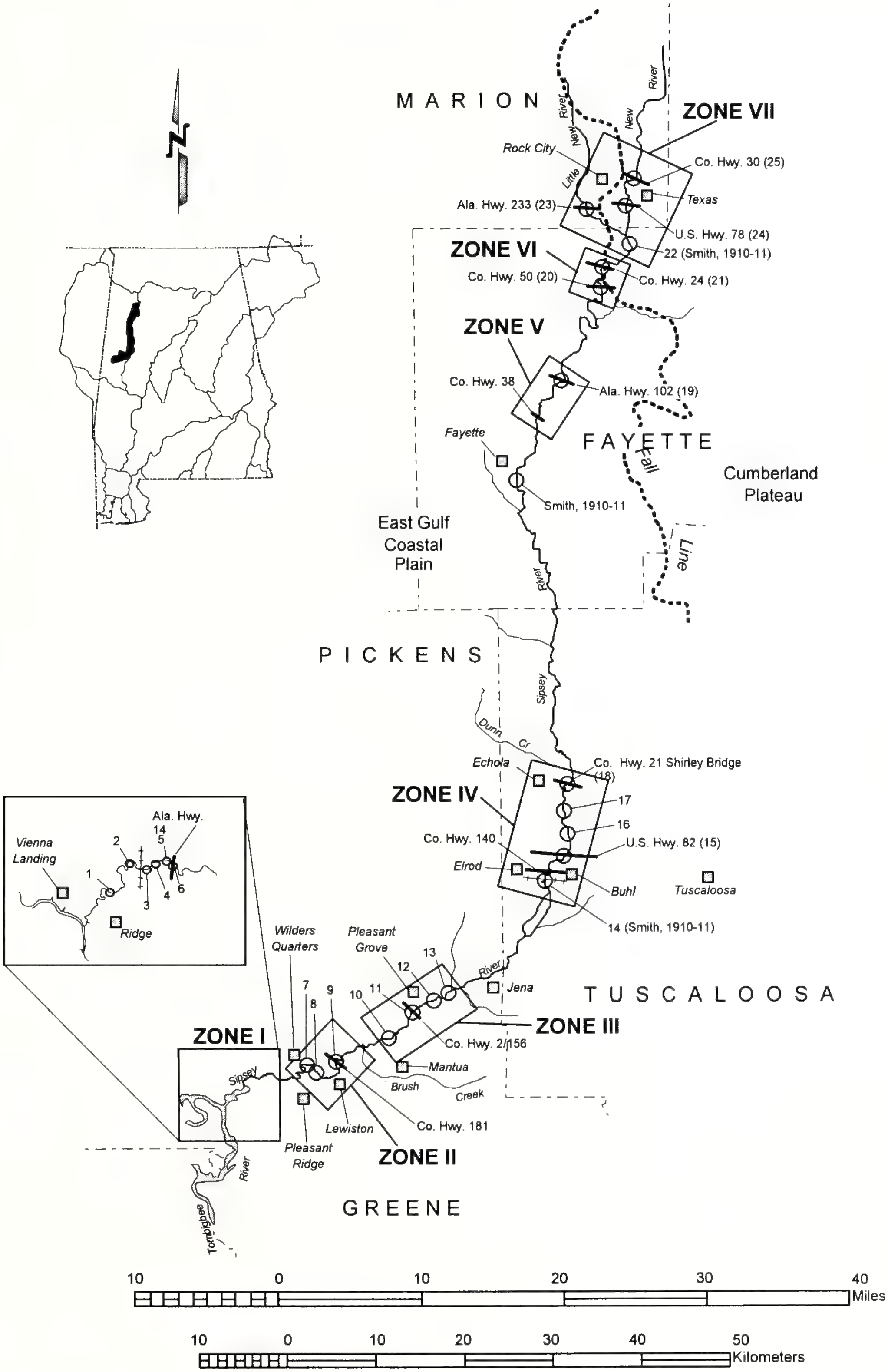
MARION
ZONE VII
Little New River
New River
Rock City
Co. Hwy. 30 (25)
Texas
Ala. Hwy. 233 (23)
U.S. Hwy. 78 (24)
22 (Smith, 1910-11)
ZONE VI
Co. Hwy. 50 (20)
Co. Hwy. 24 (21)
ZONE V
Co. Hwy. 38
Ala. Hwy. 102 (19)
Fayette
FAYETTE
Fall Line
Cumberland Plateau
Smith, 1910-11
East Gulf Coastal Plain
River
PICKENS
Sipsey
Dunn Cr
Echola
Co. Hwy. 21 Shirley Bridge (18)
ZONE IV
17
16
Co. Hwy. 140
U.S. Hwy. 82 (15)
Elrod
Buhl
Tuscaloosa
14 (Smith, 1910-11)
Vienna Landing
Ala. Hwy. 14
1
2
3
4
5
6
Ridge
Wilders Quarters
Pleasant Grove
7
8
9
10
11
12
13
River
Jena
TUSCALOOSA
ZONE III
ZONE I
Sipsey
Co. Hwy. 2/156
Mantua
Brush Creek
Lewiston
Co. Hwy. 181
Pleasant Ridge
ZONE II
River
Tombigbee
GREENE
10 0 10 20 30 40 Miles
10 0 10 20 30 40 50 Kilometers

Figure 1. Location of sampling stations and zones and significant nearby landmarks in the Sipsey River, Alabama.

Pickens/Greene county line. The Gainesville Pool of the Tennessee-Tombigbee Waterway affects the lower Sipsey River upstream to about the Alabama Hwy. 14 bridge near Aliceville, Pickens County. Near the mouth, the Sipsey is 18-30 m wide and has broad, deep, sluggish pools. Pools are separated by shoal areas with stable gravel and sand bottoms, with moderate to swift current. The lower river meanders through a wide alluvial floodplain of bottomland hardwoods. This area extends to about the US Hwy. 82 bridge in Tuscaloosa County. Above US Hwy. 82 the river is smaller and dominated by a silt or clay substrate. Gravel bars become rare, with upstream progression to its small, rocky headwater streams. Widespread clear-cutting in this area has led to destabilized banks, considerable sloughing of streamside cover, and introduction of silt/sand into the stream.

Extensive aquifer recharge of the Sipsey results in well-sustained stream flows for most of the year (McGregor and O'Neil, 1992). The stream flow of the Sipsey at Elrod, Tuscaloosa County, averages 21.92 cubic meters per second (cms) with a maximum discharge of 787.2 cms on February 3, 1961 and a minimum of 0.34 cms on September 20, 1954 (McGregor and O'Neil, 1992).

METHODS

Though the Sipsey River has several bridge crossings (Fig. 1), access is difficult in some areas. Since the majority of the river contains slow, deep water and is bordered by dense bottomland forest, one cannot easily collect by wading or shoreline surveying. These areas yield fewer unionids, except for a few slackwater species. The majority of the unionids are found around firm sand, clay or gravel riffles, shoals, or islands. In the productive lower river one may travel a mile or more between such areas. Therefore, access by jon boat or canoe is helpful in making unionid surveys. This difficult situation is compounded by the fact there are only three public boat launches in the vicinity. We used a jet-powered outboard skiff and jon boat in the lowest reach and near the Hwy. 2 ramp, and canoes elsewhere. The upper reach of the Sipsey River was surveyed by wading, often with the use of inner tubes for transportation.

Dead specimens were commonly cast up on shoals by high water or found in muskrat middens. However, we also searched for living specimens by wading and hand picking, usually by raking with our hands through the substrate or with the aid of a mask and snorkel. All living specimens collected were placed back in the substrate except a few taken for voucher specimens or for genetic study. The specimens were sorted, cleaned, labeled, and deposited in the University of Alabama (UA) Mollusk Collection. The bulk of the survey was done in 1996-1999. Collections made by one author (WHM) in 1989 and the early 1990s and by another author (JMP) in 1990-1991 were included.

Historical records were examined from all museums known to possess major unionid collections, including the Academy of Natural Sciences of Philadelphia (ANSP), Carnegie Museum of Natural History (CMNH), Florida Museum of Natural History (FLMNH), Harvard University Museum of Comparative Zoology (MCZ), The Ohio State University Museum of Biological Diversity (OSUM), University of Illinois Museum of Natural History (UIMNH), University of Michigan Museum of Zoology (UMMZ), and United States National Museum (USNM). The museum material was examined on site by one author (JDW) for all the aforementioned museums; CL also examined material at UMMZ and FLMNH. Other identifications and records were substantiated by loans from CMNH and help from G. Thomas Watters for OSUM specimens. Nomenclature used in this paper follows Turgeon *et al.* (1998) unless otherwise noted.

RESULTS

In our survey collections were made at 25 stations (Fig. 1). A total of 35 species of 22 genera and the Asian clam, *Corbicula fluminea* (Müller, 1774), were collected in different arbitrarily delineated zones of the river. Relative abundance was estimated by counting all specimens collected by McCullagh *et al.* during 1997-1999 and McGregor *et al.* during 1996-99. Since effort was concentrated in the riffle/shoal areas, the numbers of species inhabiting the slow, deep, sandy/muddy habitats were probably underrepresented.

Historical Perspective

Though some of the early 19th century malacologists collected nearby *e. g.*, T. A. Conrad [1834] described several species from Greene Co., Alabama, and A. A. Hinkley sampled the Tombigbee in 1906), there was no systematic collecting in the Sipsey until Herbert Huntington Smith sampled the river in 1910-1911. Smith was a very thorough collector who worked for a "Syndicate" of early American malacologists, including T. H. Aldrich, George H. Clapp, Henry A. Pilsbry, and Bryant Walker. Smith covered most of Alabama, and his collections were ultimately sent to several major museums (Clapp, 1920; van der Schalie, 1981). Smith concentrated his efforts in the Sipsey at three stations (Fig. 1): near Elrod, near Fayette, and the Forks of the Sipsey near Texas, Alabama.

Smith (1911) initially believed the river to be a poor stream for unionids after his initial work at the Forks. However, he later realized that the Sipsey is "one of the richest in Alabama, and decidedly peculiar" (p. 84). "Most of it is 'dead water,' with a steady, pretty strong current and three or four feet deep; it is very crooked and choked with drift logs. Now and then there are gravel shoals, shallow, with an even, strong current, and these are the places for the mussels, especially *Pleurobemas*" (p. 84).

Smith found a total of 24 species from the three stations combined. There were four species taken by H. H. Smith (*Anodontoides radiatus, Quadrula metanevra, Toxolasma parvus*, and *Uniomerus tetralasmus*) that we did not find. *A. radiatus*, however, was collected near Elrod in 1981 (Appendix). Thirteen unionid species were collected recently that were not found by Smith *(Amblema plicata, Anodonta suborbiculata, Lasmigona complanata alabamensis, Ligumia recta, Megalonaias nervosa, Potamilus inflatus, P. purpuratus, Pyganodon grandis, Q. apiculata, Q. stapes, Q. rumphiana, Truncilla donaciformis*, and *Utterbackia imbecillis*). Virtually all of these species, however, occur exclusively in the lower Sipsey or may have recently colonized the locality near Elrod.

Regrettably, because the lowermost Sipsey was not surveyed historically and is now impounded, it is uncertain whether some endangered unionids known to inhabit the Tombigbee were ever established there. These include *Pleurobema taitianum, P. marshalli* Frierson, 1927, *Epioblasma penita* (Conrad, 1834) and *Quadrula stapes* (Williams *et al.*, 1992; USFWS, 1987). We did not find any of these taxa in our study, however, a single record was reported for *P. taitianum* in the lower Sipsey in 1984 and two records of *Q. stapes* were reported, one each in 1984 and 1987 (Appendix).

Species Accounts and Discussion

There are records or reports of 42 species of unionid bivalves plus the introduced Asian clam from the Sipsey River. Here we provide brief species accounts including notes on habitat, rangewide and local distribution, and conservation status. The general distributional data were compiled from Clench and Turner (1956); Parmalee (1967); Johnson (1970); Gordon *et al.* (1980); Oesch (1984); Cummings and Mayer (1992); Bogan (1993b); Vidrine (1993); Hartfield (1994); Williams and Butler (1994); Watters (1995); Howells *et al.* (1996); and Parmalee and Bogan (1998). For the Mobile Basin distribution we used van der Schalie (1938); Hurd (1974); van der Schalie (1981), Williams *et al.* (1992); Parmalee and Bogan (1998); and McGregor *et al.* (1999). The conservation status of each species was obtained from Williams *et al.* (1993) and Lydeard *et al.* (1999) and is noted at the end of each account.

1. *Amblema plicata* (Say, 1817) - The threeridge was commonly encountered in the lower Sipsey. This taxon name was used since its former designation, *A. perplicata* (Conrad, 1841), cannot be distinguished using mitochondrial DNA sequence data (Mulvey *et al.*, 1997). It was found in firm bottom in slow to moderate current. Recruitment was noted with some 30-40 mm juveniles found. *A. plicata* is abundant in the lower Sipsey, and van der Schalie (1981) listed the species as one Smith documented near Elrod (Appendix). We were unable to locate that specimen. *A plicata* is found from the Escambia River, Florida, west to the Guadalupe River, Texas, and northward throughout the Interior Basin. In the Mobile Basin it is found in the Tombigbee drainage and in the Cahaba River, but in the Coosa there is a genetically distinct entity referred to as *A. elliottii* (I. Lea, 1856) (Mulvey *et al.*, 1997). McGregor *et al.* (1999) did not find the species in other Tombigbee River tributaries. Currently stable.

2. *Anodonta suborbiculata* Say, 1831 - The flat floater was rare in the river, found only in an oxbow at station 14 and a slough at station 11. However, our survey of the sluggish, muddy backwaters favored by this genus was incomplete. This species was not previously reported from the Sipsey, possibly reflecting recent colonization since impoundment. Indeed, its range expansion from introduction of host fishes and impoundment has been documented throughout the eastern U.S. (B. E. Sietman *et al.*, unpubl. data). This species is reported from the Escambia River, Florida, west to the Brazos River in east Texas and north in the southwestern portion of the Interior Basin to Indiana and Minnesota (Havlik, 1981). One author (SWM) has recently collected the species in the lower Buttahatchee River, Mississippi (unpubl. data). Currently stable.

3. *Anodontoides radiatus* (Conrad, 1834) - The southern creekshell was not found during the present survey but was taken by H. H. Smith in 1910, Koch in 1981 (Appendix), and noted in a status survey for the endangered *Quadrula stapes* (Pierson, 1991). We found one specimen in the CMNH which was labeled as *Strophitus subvexus* (Conrad, 1834) but was actually *A. radiatus* (CMNH 61-837; Appendix). It is a small river or creek species that may have been in tributaries that were not sampled. It is an endemic eastern Gulf drainage region found from the Apalachicola River drainage in Florida to east of the Mississippi River in Louisiana . Special concern.

4. *Arcidens confragosus* (Say, 1829)- A single dead specimen of *Arcidens confragosus* was found in the lower Sipsey River by Pierson (1991). This species is known to occur in the impounded Tombigbee and Black Warrior rivers, so this is not surprising. We did not survey the impounded lower reach of the Sipsey, but this species might possibly be present. Currently stable.

5. *Ellipsaria lineolata* (Rafinesque, 1820) - The butterfly was found only rarely in riffles of the lower Sipsey, though recruitment must be occurring since 30 mm specimens were found. This species is widespread in the Interior Basin, but is not found in western Gulf drainages south of the Arkansas River. It ranges north to Minnesota and east to Ohio. In the Mobile drainage, its southeastern limit, it is currently found in the Cahaba and was found in the Coosa and Tombigbee rivers. Special concern (nationally), Currently stable (Alabama).

6. *Elliptio arca* (Conrad, 1831) - The Alabama spike was common in the lower Sipsey in gravel substrata with moderate to swift current. Good recruitment was noted with several small (ca. 40 mm) specimens found. It is an eastern Gulf drainage regional endemic and appears to be more common in the Sipsey than anywhere else in the Mobile Basin, being uncommon in the Coosa, and rare in the Cahaba. Threatened (nationally), Imperiled (Alabama).

7. *Elliptio arctata* (Conrad, 1834) - The delicate spike was found at one station in the lower Sipsey. Hurd (1974) reported *E. arctata* to be abundant in the headwaters of the Coosa, and to occur in a unique habitat, packed together vertically under large rocks in swift water. It is found discontinuously from the Pearl River system east to the Escambia and Apalachicola drainages and possibly north on the Atlantic Slope to the Santee-Cooper, Cape Fear, and Savannah drainages, though the latter records are doubtful (Parmalee and Bogan, 1998). Special concern.

8. *Elliptio crassidens* (Lamarck, 1819) - The elephantear was common in the lower river from Hwy. 82 downstream to Hwy. 14 in swift current with a sandy to firm, fine gravel or clay substrate, not in heavy gravel as most other species. In general, it ranges from the Apalachicola drainage west to Louisiana, east of the Mississippi River, then north throughout the Interior Basin. It was common in the Mobile Basin though rare in impoundments. It was not found in tributaries of the lower Tombigbee River by McGregor *et al.* (1999). It seems to be a sediment-tolerant species and is now very abundant in the mid-Cahaba River, which has suffered a serious decline of other unionid species (SWM, unpubl. data). It was found in the Tombigbee both before and after impoundment, and was found in the Sipsey up to the historic station near Elrod (Appendix). Currently stable.

9. *Fusconaia cerina* (Conrad, 1838) - The Gulf pigtoe is abundant in the Sipsey throughout the lower river from Hwy. 82 downstream to Hwy. 14. It is somewhat variable, with some shells showing anteriorly turned beaks, like *Pleurobema taitianum*, and nacre color varying from silver to rose. It was found in gravel in moderate current. Recruitment was excellent, with many juveniles collected. It is another eastern Gulf drainage endemic ranging from the Mobile Basin to Louisiana, east of the Mississippi River. It was not found in tributaries of the lower Tombigbee River by McGregor *et al.* (1999). Currently stable.

10. *Fusconaia ebena* (I. Lea, 1831) - The ebonyshell is rare in the Sipsey and was limited to riffle areas in the lower river downstream of Hwy. 2. Herbert H. Smith collected the ebonyshell from the upper Sipsey near the Forks. It is a widespread species found throughout the Interior Basin east of the Mississippi River, east to the Mobile Basin. Currently stable.

11. *Lampsilis ornata* (Conrad, 1834) - The southern pocketbook was abundant in the Sipsey throughout the middle and lower river from Hwy. 82 downstream to Hwy. 14. It was found in fast water, deeply buried in heavy gravel. Recruitment appears excellent in the Sipsey. It is another eastern Gulf regional endemic found in the Escambia River and west throughout the Mobile Basin to Louisiana, east of the Mississippi River. It was not found in tributaries of the lower Tombigbee River by McGregor *et al.* (1999). Special concern.

12. *Lampsilis perovalis* (Conrad, 1834) - The orangenacre mucket was fairly common, distributed in the river from Hwy. 82 downstream to Hwy. 14. Like *L. ornata*, it was found deeply buried in heavy gravel in moderate to swift current. The species is a Mobile Basin endemic and exists in only a few scattered locations, including the Sipsey Fork, North River, Cahaba River, and Sipsey River. Recruitment was noted with several 50 mm juveniles found. The species is listed federally as Threatened (USFWS, 1993). Threatened.

13. *Lampsilis straminea claibornensis* (I. Lea, 1838) - The southern fatmucket was common in the Sipsey in slow, sandy areas, and along the upstream and downstream margins of gravel riffles. Good recruitment was noted with many juveniles found. Some specimens from rough substrate had periostracum resembling the striated surface texture of *L. s. straminea*, which may be an ecotype. *L. s. claibornensis* is another eastern Gulf regional endemic found from the Suwannee River drainage, Florida, to Louisiana, east of the Mississippi River. It is common throughout the Mobile Basin, especially in creeks or small rivers. Currently stable.

14. *Lampsilis teres* (Rafinesque, 1820) - The yellow sandshell was common throughout the middle and lower river.

Like *L. s. clabornensis*, it favors sandy substrates in slow water. Several juveniles were noted. The species is distributed from the Gulf drainages of Florida from the Hillsborough River system north and westward to the Rio Grande, Texas. It is also found throughout the Interior Basin north to Canada and east in the Ohio drainage. Currently stable.

15. *Lasmigona complanata alabamensis* Clark, 1985 - The Alabama heelsplitter was uncommon and restricted to the lower Sipsey, but recruitment was noted with the presence of subadults. It is found in the Mobile Basin in Alabama, Georgia, and Mississippi. Special concern.

16. *Leptodea fragilis* (Rafinesque, 1820) - The fragile papershell was widespread and common in the river from Hwy. 82 downstream to Hwy. 14. It displayed a wide habitat tolerance, and was found in slow areas of riffles and in sand and mud in slack water areas. *L. fragilis* was rarely found alive (only 2 specimens) possibly due to its tendency to burrow deep into the substratum, but recruitment must be occurring as many shells of small juveniles were found. It is another wide-ranging species found throughout the Mississippi River system north and east to the St. Lawrence River system, and west to Texas. It survives in reservoirs and some tributaries of the lower Tombigbee in Alabama (Hurd, 1974, Williams *et al.*, 1992; McGregor *et al.*, 1999). Currently stable.

17. *Ligumia recta* (Lamarck, 1819) - A single live black sandshell was found in the Sipsey River near Hwy. 181, Greene County, representing a new tributary record for the species. It is widely distributed throughout the Mississippi Basin from Minnesota to western New York and Pennsylvania, southwest to Oklahoma, east to the Mobile drainage, and north to the St. Lawrence drainage. Special concern.

18. *Medionidus acutissimus* (I. Lea, 1831) - The Alabama moccasinshell was rare and restricted to the lower Sipsey from near the Hwy. 23 bridge upstream to Hwy. 82. It is a Mobile Basin endemic and the paucity of records is likely due to the difficulty of finding such a diminutive species in turbid water. It was also known from the headwaters of the Black Warrior, Tombigbee, Cahaba, and Coosa systems. It is a small river species and intolerant of impounded conditions. The species is listed federally as threatened (USFWS, 1993). Threatened.

19. *Megalonaias nervosa* (Rafinesque, 1820) - The washboard was common in the lower Sipsey, often found living in small beds in quiet water and the head or tail of riffles. It was fairly large in the Sipsey, reaching at least 175 mm in length. It is widespread in the Interior Basin and west to the Rio Grande, Texas. It was most common in the lower river downstream of Hwy. 2, which is expected as this species is known as a "large river" inhabitant. It appears to be reproducing in the Sipsey; several small- to medium-sized juveniles were found. It was found alive at most stations where it was encountered. Currently stable.

20. *Obliquaria reflexa* (Rafinesque, 1820) - The threehorn wartyback was common in the Sipsey downstream of Hwy. 82, but most common in the lower river downstream of Hwy. 2. It is a widespread species in the Interior Basin, west to Texas and northeast to Ohio, and the Mobile Basin. Currently stable.

21. *Obovaria jacksoniana* (Frierson, 1912) - The southern hickorynut was common, but much less common than its congener, *Obovaria unicolor*. *Obovaria jacksoniana* was found sparsely throughout the middle to lower river. Its habitat was gravel riffles in moderate current. Some recruitment was evident but not as obvious as *O. unicolor*. *Obovaaria jacksoniana* is widespread throughout the Mobile Basin and ranges west to the Neches and Sabine rivers in east Texas. It is found north to eastern Arkansas and the Missouri River and to west Tennessee. Interestingly, Williams *et al.* (1992) did not find it in the main channel of the Tombigbee River, pre- or post-impoundment. It was found in a tributary of the lower Tombigbee River by McGregor *et al.* (1999). Special concern.

22. *Obovaria unicolor* (I. Lea, 1845) - The Alabama hickorynut was common in the Sipsey as far upstream as Hwy. 82 but was most common in moderate to fast water gravel riffles in the lower river. This species is another eastern Gulf regional endemic, found from the Mobile Basin west to Louisiana, east of the Mississippi River. In the Mobile Basin it was common in the Tombigbee prior to impoundment, but nearly absent afterward. It was rare in the Cahaba and Coosa drainages. Special concern.

23. *Plectomerus dombeyanus* (Valenciennes, 1827) - A single dead specimen of *Plectomerus dombeyanus* was found in the lower Sipsey River by Pierson (1991) and a single specimen from the lower river is in the MMNS collection (Appendix). It is known to occur in the impounded Tombigbee and Black Warrior rivers, so this is not surprising. We did not survey the impounded lowest reach of the Sipsey, but this species might possibly be present. Currently stable.

24. *Pleurobema decisum* (I. Lea, 1831) - The southern clubshell was the second most abundant species in the Sipsey and was found in both fast and slow water portions of riffles consisting of fine to coarse gravel and clay.

Although it was found throughout the river below Hwy. 140, it was most common in the lower river near Hwy. 14. An amazing 114 specimens were tallied there on one trip, including 21 specimens in one large midden. This species displayed excellent recruitment, with large numbers of juveniles frequently noted. This Mobile Basin endemic was once common throughout the basin, but is now found only in Bogue Chitto, Bull Mountain, Chewacla, and Lubbub creeks, the Buttahatchee River, and the Coosa River below Weiss Dam. Van der Schalie (1938) reported it was the most abundant *Pleurobema* in the Cahaba, but based on recent surveys it is evident the Sipsey River supports the largest population of *P. decisum* today. The species is federally listed as Endangered (USFWS, 1993).

25. *Pleurobema perovatum* (Conrad, 1834) - The ovate clubshell was common throughout the lower river up to Hwy. 140. Unlike *P. decisum*, it appeared most common in mid-river. At one area below the railroad bridge downstream of Hwy. 140 we tallied 17 specimens from middens (there were 30 *P. decisum* there). Subadult specimens of these two taxa are easily confused, but *P. perovatum* is more ovate with more centrally located beaks, and the pseudocardinal teeth are smaller with slightly different orientation. This is another federally endangered (USFWS, 1993) Mobile Basin endemic, and the Sipsey is probably its best refugium as it is declining elsewhere. Endangered.

26. *Pleurobema taitianum* (I. Lea, 1834) - The heavy pigtoe was not found in the present survey, but records of the species in the Sipsey have been documented (Pierson, 1991; Appendix). It is endemic to the Coastal Plain portion of the Mobile Basin. Prior to impoundment, this species was not uncommon in the main channel of the upper Tombigbee River, where it was collected at 17 localities between Epes, Alabama, and the mouth of Tibbee Creek, northwest of Columbus, Mississippi (Williams, 1982). *P. taitianum* inhabited gravel shoals in large rivers with moderate currents. It is federally listed as Endangered (USFWS, 1987).

27. *Potamilus inflatus* (I. Lea, 1831) - A single specimen of the inflated heelsplitter was found during the present survey in the Sipsey River near Hwy. 14. It was known to exist in the Tombigbee River pre-impoundment and it likely represents a waif dispersal event. It is found from the Alabama River west to the Amite River of Louisiana, although the western population is genetically distinct (Roe and Lydeard, 1998). The species is federally listed as Threatened (USFWS, 1990).

28. *Potamilus purpuratus* (Lamarck, 1819) - The bleufer was common in the entire river but more commonly collected in the lower reaches. However, it was one of the few species we found upstream in the silted area in Fayette County. It is found in slower currents and was associated with *Amblema plicata* and *Megalonaias nervosa* in firm mud to clay substrate along river banks upstream and downstream of riffles. It is found as far west as south Texas and in the southern portion of the Interior Basin, however, recent doubts have been cast regarding the taxonomy and distribution of *P. purpuratus* (J. Serb and C. Lydeard, unpubl. data). It was not reported in the Sipsey by H. H. Smith, but now occurs throughout the river. Currently stable.

29. *Pyganodon grandis* (Say, 1829) - The giant floater was rare in the Sipsey, but the sluggish backwaters favored by this genus were not surveyed extensively. This is a widespread species found from the Ochlockonee River, Florida, to the Rio Grande, Texas, and throughout the Interior Basin. Currently stable.

30. *Quadrula apiculata* (Say, 1829) - The southern mapleleaf was rare in the Sipsey and restricted to the lower river. It is found in all Gulf drainages from the Mobile system to the Rio Grande, and has been introduced as a commercial species in the southeastern U. S. (Parmalee and Bogan, 1998; Garner and McGregor, 2000). It is possible this taxon may intergrade with *Q. rumphiana*. Currently stable.

31. *Quadrula aspera* (I. Lea, 1831) - The Gulf mapleleaf is also rare in the Sipsey. Only one specimen was found on the most downstream shoal in the river below Hwy. 14. Much confusion exists over this taxon, as many workers (Burch, 1975; Turgeon *et al.*, 1998) refer it to the previous species or not at all. However, shell differences are present as *Q. aspera* has a deep central sulcus bordered by a row of pustules extending from the ventral margin of the shell to the umbonal tip. Taxonomic work is needed to further define this complex. In the Mobile Basin it is common in the Coosa River impoundments, the lower Cahaba River, the Noxubee River, and the Alabama River (Hurd, 1974; W. H. McCullagh, pers. obs.; S. W. McGregor, unpubl. data).

32. *Quadrula asperata* (I. Lea, 1861) - The Alabama orb was by far the most abundant unionid in the Sipsey and was collected throughout the lower and middle reaches of the river. It was widely distributed in the Coastal Plain portion of the Mobile Basin and above the Fall Line in the Black Warrior, Coosa, and Cahaba river systems. It is absent above the Fall Line in the upper Tallapoosa, where a related species, *Q. archeri* Frierson, 1905, is found. Currently stable.

33. *Quadrula metanevra* (Rafinesque, 1820) - The monkeyface is known from the Sipsey based on a single record from the CMNH from H. H. Smith's 1910-1911 collection.

It was not found during any subsequent survey including our own field work. We verified the specimen (CMNH 61-7225; Appendix) and it may represent either a locality error or a rare dispersal event. It was common in the Tombigbee prior to impoundment (Williams *et al.*, 1992). It is widespread in the Interior Basin and in the Mobile Basin. In the latter it was common in the Tombigbee, Alabama, and Coosa rivers prior to impoundments. It is still common in the lower Cahaba (W. H. McCullagh *et al.*, pers. obs.; S. W. McGregor, unpubl. data). Currently stable.

34. *Quadrula rumphiana* (I. Lea, 1852) - The ridged mapleleaf was very common in the Sipsey and found throughout the river, although not in great abundance from Hwy. 82 upstream. Herbert H. Smith did not find it in his surveys, so it is possible the upstream populations represent a recent colonization. It was found in the Tombigbee prior to impoundment (Williams *et al.*, 1992). This Mobile Basin endemic is common in small rivers and creeks. The species was collected and identified by other recent workers as *Q. apiculata*, but it is distinguished from its congeners by its high, trigonal shape with a prominent posterior ridge, unadorned by pustules. Our identification of *Q. rumphiana* was substantiated by comparison to the holotype (USNM 84189). Hurd (1974) made the observation that the species tolerates impoundment and is common in the Coosa reservoirs. Special concern.

35. *Quadrula stapes* (Lea, 1831) - The stirrupshell was not collected from the Sipsey during our study and was not found during a recent species status survey (Pierson, 1991). It is an endemic of the Tombigbee and Alabama rivers. Williams *et al.* (1992) found it to be fairly common in the Tombigbee prior to impoundment, but it was absent after the river was impounded. Smith did not record this species in his survey. One specimen was taken from the Sipsey near Hwy. 23 by Stansbery in 1987 (OSUM 29049; verified by G. Thomas Watters) and one near Hwy. 23 by Hartfield, et al. in 1984 (Appendix). The species is federally listed as Endangered (USFWS, 1987) and presumed extinct.

36. *Strophitus subvexus* (Conrad, 1834) - The southern creekmussel was extremely rare in the Sipsey, observed only in the lower river in slow, muddy areas. *Strophitus subvexus* is an eastern Gulf drainage regional endemic, found from the Apalachicola River, Florida to Louisiana. Special concern.

37. *Toxolasma parvus* (Barnes, 1823) - The lilliput was not found in our survey, but several were taken by H. H. Smith and referred to *Carunculina cromwelli* (Lea, 1865). We examined these specimens (CMNH; Appendix) and referred them to *Toxolasma parvus*. They were taken in the upper river. This is a wide-spread species found from Florida to Texas and north throughout the Mississippi drainage. This small species may simply have been overlooked by the method of our survey, but is certainly not abundant if it still occurs in the river. Currently stable.

38. *Tritogonia verrucosa* (Rafinesque, 1820) - The pistolgrip was collected throughout the Sipsey but was most abundant in the middle and lower river from Hwy. 82 downstream to Hwy. 14, and slightly more common in the lower reaches below Hwy. 2. The Sipsey specimens were small for this species, seldom exceeding 120 mm in length. As noted for Cahaba River specimens by van der Schalie (1938) and upper Coosa specimens by one author (SWM, pers. obs.), some specimens have purple nacre and some have white. It is known in the Interior Basin from east Texas north to Minnesota and east to Pennsylvania and in the Mobile Basin. Currently stable.

39. *Truncilla donaciformis* (I. Lea, 1828) - A single relic shell of the fawnsfoot was found downstream of Hwy. 14. This species is typically found in the main channel of large rivers, which probably explains its rarity in the Sipsey River. Most collections of this species in the upper Tombigbee River consisted of fewer than five individuals at any one station. It is known in the Interior Basin from east Texas north to Minnesota and Michigan and east to Pennsylvania and in the Mobile Basin. Currently stable (nationally), Imperiled (Alabama).

40. *Uniomerus tetralasmus* (Say, 1830) - The pondhorn was not found in our survey, but two specimens were taken by Smith in Fayette County. We examined these specimens (CMNH 61-8366; Appendix) and concurred with the identification. It favors mud-bottom lakes, pools, sloughs, and oxbows (Oesch, 1995) and may have been overlooked in our study. It is found from the Mobile Basin west to the Trinity River, Texas, and is widespread in the Interior Basin. Currently stable.

41. *Utterbackia imbecillis* (Say, 1829) - The paper pondshell was rare in the Sipsey with only a single juvenile found in a sandy area at Hwy. 82. It was not previously reported in the Sipsey River, but the absence of records of this species is most likely due to the paucity of collections from oxbow lakes and backwater areas. As mentioned previously, the anodontines may be recent introductions since impoundment. This species is one of the most widely distributed unionids, found up the Atlantic Slope to Pennsylvania, west to the Rio Grande, and throughout the Interior Basin. Currently stable.

42. *Villosa lienosa* (Conrad, 1834) - The little spectaclecase was abundant throughout the river but favored slow, sand/mud habitats. It was found far upstream in the headwaters in the New River, Marion County. Good recruitment was noted. It is found from the Suwannee River, Florida, to the San Jacinto River, Texas, and north in the Mississippi drainage to southwest Ohio. Currently stable.

43. *Villosa vibex* (Conrad, 1834) - The southern rainbow was rare in the Sipsey, found in slow backwater areas throughout the middle to lower river from Hwy. 82 downstream to Hwy. 14. This species inhabits streams ranging from small creeks to large rivers but is usually more common in creeks than rivers. It is another regional endemic found in southeast Georgia and northeast Florida, and west to the Gulf drainages of Louisiana, east of the Mississippi River. Currently stable.

Others: The exotic Asian clam was not counted in this survey, however, it is clearly part of the bivalve fauna of the Sipsey. It appeared to be more common in the upper and middle reaches than the lower reaches of the river.

Conclusions and Recommendations

Thirty-five species of 22 genera were found in this study, and an additional 7 species were found in museum collections for a total of 42 species. There were 5 Mobile Basin endemics and 12 Gulf drainage regional endemics (46% total). Seven species (*Anodonta suborbiculata, Elliptio arctata, Fusconaia ebena, Ligumia recta, Potamilus inflatus, Strophitus subvexus*, and *Truncilla donaciformis*) that were collected recently were very rare (represented by five or fewer specimens). Three species (*Anodontoides radiatus, Quadrula metanevra* and *Uniomerus tetralasmus*) that were collected by H. H. Smith were represented by only one or two specimens and *Toxolasma parvus* by seven specimens. *Quadrula stapes*, which was collected in 1987, was represented by only one specimen. If we exclude these rare taxa, the Sipsey mussel fauna is comprised of 31 common to abundant species, 25 of which were collected alive.

The Sipsey River currently serves as an unprotected refuge to nine species that are of special concern, two imperiled in Alabama (*Elliptio arca* and *Truncilla donaciformis*), three that are federally listed as threatened (*Lampsilis perovalis, Medionidus acutissimus* and *Potamilus inflatus*), and three that are federally listed as endangered (*Pleurobema decisum, P. perovatum*, and *Quadrula stapes*). Of these, *P. inflatus, Q. stapes*, and *T. donaciformis* are known from a single specimen each, however; the remaining taxa appear to be rather common.

One notable and disturbing difference between the H. H. Smith collection and recent collections is the decrease in the number of species found in the upper Sipsey. Smith documented 15 species near Fayette and 16 species at the Forks. We observed only three species near Fayette and only four at the Forks. We noted the influence of agricultural, mining, and silvicultural activities and fewer habitats, and silting in of these habitats, as did Pierson (1991). Several species thought to be more sensitive to silt conditions are now absent in these areas, including *Elliptio arca, Medionidus acutissimus, Obovaria unicolor, O. jacksoniana, Pleurobema decisum*, and *P. perovatum.*

No detailed land use study has been conducted on the Sipsey River, but clearly studies are needed to determine what activities may have eliminated these species from the upper reaches. Given the results of qualitative sampling during the study, it is imperative that more quantitative studies be conducted in several locales to ascertain species densities and establish base-line data. Subsequent changes in densities can be monitored on a regular basis every three to five years to detect any changes and determine whether any potential land-use activities are having a negative impact on the fauna.

We recommend protection of this freshwater bivalve fauna by following an entire watershed approach (*e.g.*, Shute *et al.*, 1997; Burkhead *et al.*, 1997). Conservation should focus on the ecosystem and watershed level instead of individual species. The general public needs to be educated about the value and significance of ecosystem protection, and management will require the cooperation and coordination of all stakeholders. The Sipsey Swamp (downstream of U.S. Hwy. 82) was recently recognized as one of Alabama's natural wonders by the non-profit Alabama Environmental Council. In addition, the Forever Wild program of the State Lands Division of the Alabama Department of Conservation and Natural Resources purchased 3,000 acres of the Sipsey Swamp along the east bank of the river near Buhl, Tuscaloosa County, and 500 acres near Hwy. 82 are owned by the Alabama Department of Transportation (Ken Wills, unpubl. data). The latter area serves as a wetland mitigation preserve. The Sipsey River was proposed for protection by inclusion as a National Wild and Scenic River in 1968 by the Alabama Water Improvement Commission (now Alabama Department of Environmental Management). However, the proposal was rejected and a portion of the Sipsey Fork of the Black Warrior River is the only stream in Alabama recognized under the Act (McGregor and O'Neil, 1992).

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APPENDIX

Museum records representing the historic Sipsey River unionid bivalve fauna including the H. H. Smith Collection of 1910-1911 and subsequent published and unpublished species status surveys.

Abbreviations: CMNH - Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.
FLMNH - Florida Museum of Natural History.
OSUM - Ohio State University Museum of Biological Diversity.
ANSP - Academy of Natural Sciences of Philadelphia.
MCZ - Museum of Comparative Zoology, Harvard University.
MMNS - Mississippi Museum of Natural Science
UIMNH - University of Illinois Museum of Natural History
UMMZ - University of Michigan Museum of Zoology.
USNM - United States National Museum (Smithsonian).

Note: Numbers in parentheses indicate numbers of specimens from each lot, if known.

1. *Amblema plicata*
FLMNH 197551 (1) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
FLMNH 197556 (2) Hwy. 23, M. Pierson, 6 July 1990.
FLMNH 197677 (2) Hwy. 14, M. Pierson, 14 Nov. 1991.
FLMNH 197763 (5) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
FLMNH 197808 (2) Greene Co., Pierson and Hartfield, 26 Sep. 1991.
FLMNH 197819 (1) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
FLMNH 207960 (8) Hwy. 2, Pierson and Hartfield, 27 Sep. 1991.
MMNS 2022 (7) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 2802 (4) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.
MMNS 4914 (1) Hwy. 14, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 5145 (5) Hwy. 23, Hartfield, Stewart, Williams, 11 Sep. 1984.
van der Schalie (1981) noted Smith recorded *A. perplicata* from the Sipsey near Elrod, but we were unable to find the specimen.

3. *Anodontoides radiatus*
CMNH 61-8378 (1) The Forks, Texas, Marion County, H. H. Smith, 1910.
OSUM 50208 (1) Elrod, L. Koch, 10 Oct. 1981.

5. *Ellipsaria lineolata*
ANSP 100578 The Forks, Texas, Fayette County, H. H. Smith. (1)
FLMNH 197574 (2) Hwy. 2, Pierson and Hartfield, 27 Sept. 1991.
FLMNH 197751 (1) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
MMNS 2011 (1) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.

6. *Elliptio arca*
ANSP 100609 (4) Fayette, H. H. Smith, 1910.
CMNH 61-8322 (2) Elrod, H. H. Smith 1 Sep. 1911.
CMNH 61-8323 (4) Fayette, H. H. Smith 1910.
MMNS 2013 (2) Hwy. 23, Hartfield Williams, Stewart, 12 Sep. 1984.
MMNS 2789 (6) Hwy. 23, Hartfield, Jones, Majure, 10 Aug. 1988.
MMNS 4631 (1) Sipsey River, Clay Moore, 1 Sep. 1990.
UMMZ 96496 (4) Fayette, H. H. Smith,
UMMZ 96501 (5) Elrod, H. H. Smith 1910.

7. *Elliptio arctata*
CMNH 61-8350 (9) The Forks, Texas, H. H. Smith, 1910.
MMNS 2783 Hwy. 23, P. Hartfield *et al.*, 1988.
UMMZ 94059 The Forks, Texas, H. H. Smith.
UMMZ 94061 Elrod, H. H. Smith, Sep. 1911.

8. *Elliptio crassidens*
MMNS 4909 (1) Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.
UMMZ 96558 Elrod, H. H. Smith.
UMMZ 163830 Elrod, H. H. Smith, Sep. 1911.

9. *Fusconaia cerina*
CMNH 61-8176 (10) The Forks, Texas, H. H. Smith 1910-11.
CMNH 61-8177 (6) Fayette, H. H. Smith.
CMNH 61-8178 (3) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 65105 (3) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 65131 (3) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 65137 (12) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 65140 (3) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 65195 (7) Elrod, H. H. Smith, 2 Oct. 1911.
FLMNH 65200 (3) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 65201 (2) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 65203 (4+1) Elrod H. H. Smith, 1 Sep. 1911.
MCZ 100967 (1) The Forks, Texas, H. H. Smith 1910-11.
MCZ 101848 (8) Elrod, H. H. Smith, 1 Sep. 1911.
MCZ 146644 (2) Elrod, H. H. Smith, 1 Sep. 1911.
MCZ 269626 (6) Elrod, H. H. Smith, 1 Sep. 1911.
MCZ 28473 (3) Elrod, H. H. Smith, 1 Sep. 1911.
MMNS 2019 (21) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 2792 (19) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.
MMNS 4582 (2) Sipsey River, Greene County, 22 July 1991.
UMMZ 113454 Elrod, H. H. Smith, Sep. 1911.
UMMZ 113471 The Forks, Texas, H. H. Smith.
UMMZ 113472 Fayette, H. H. Smith.
USNM 738162 (9) Elrod, H. H. Smith, 1 Sep. 1911.

10. *Fusconaia ebena*
FLMNH 197758 (1) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
MMNS 5143 (1) Hwy. 23, Hartfield, Williams Stewart, 11 Sep. 1984.
UMMZ 93004 (1) The Forks, Texas, H. H. Smith, 1910-11.

11. *Lampsilis ornata*
CMNH 61-8558 (2) Elrod, H. H. Smith, 1 Sep. 1911.
CMNH 61-8559 (1) Fayette, H. H. Smith, 1910-11.
MCZ 91264 (2) Elrod, H. H. Smith, 1 Sep. 1911.
MMNS 2089 (6) Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.
MMNS 2801 (1) Hartfield, Jones, Majure, 19 Aug. 1998.
MMNS 4901 (6) Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.
MMNS 4912 (2) Hwy. 14, Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.
UMMZ 84006 (1) The Forks, H. H. Smith, 1910-11.
UMMZ 84010 (1) Elrod, H. H. Smith, 1 Sep. 1911.

12. *Lampsilis perovalis*
CMNH 61-8543 (2) Elrod, H. H. Smith, 1 Sep. 1911.
MCZ 277579 (4) Elrod, H. H. Smith, 1 Sep. 1911.
MMNS 2014 (1) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 2086 (2) Hwy. 23, Hartfield, Stewart, Williams, 12 Sep. 1984.
MMNS 2784 (1) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1998.
MMNS 2797 (4) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.
MMNS 4903 (4) Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.

OSUM 45710 (1) Hwy. 82, L. and W. Starnes, 3 Sep. 1978.
OSUM 50239 (2) Hwy. 21/ Brownville, L. Koch, 10 Oct. 1981.

13. *Lampsilis straminea claibornensis*
ANSP 100669 (16) Fayette, H. H. Smith (?), 1911.
CMNH 61-8525 (5) Elrod, H. H. Smith, 1 Sep. 1911.
CMNH 61-8526 (11) Fayette, H. H. Smith, 1910-11.
CMNH 61-8527 (14) The Forks, Texas H. H. Smith, 1910-11.
CMNH 61-8528 (1) Ballard Cr., H. H. Smith, 1910-11.
UMMZ 62286 (1) Fayette, H. H. Smith, 1910-11.
UMMZ 83924 (7) The Forks, Texas H. H. Smith, 1910-11.
UMMZ 83926 (3) Fayette, H. H. Smith, 1910-11.
UMMZ 83930 (5) Elrod, H. H. Smith, 1 Sep. 1911.
UMMZ 163833 (2) Elrod, H. H. Smith, 1 Sep. 1911.

14. *Lampsilis teres*
CMNH 61-8517 (4) Elrod, H. H. Smith, 1 July 1912.
CMNH 61-8518 (2) Fayette, H. H. Smith, 1910-11.
MMNS 2787 (2) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.
UMMZ 83108 Elrod, H. H. Smith, Sep. 1911.

15. *Lasmigona complanata*
FLMNH 197756 (1) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
MMNS 2798 (1) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.

16. *Leptodea fragilis*
FLMNH 65910 (1) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 197537 (1) Hwy. 82, Pierson and Puleo, 29 Sep. 1990.
FLMNH 197547 (1) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
FLMNH 197555 (1) Hwy., 23, M. Pierson, 6 July 1990.
FLMNH 197583 (2) Hwy. 2, Pierson and Hartfield, 27 Sep. 1991.
FLMNH 197828 (1) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
MMNS 2799 (1) Hwy. 23, Hartfield, Jones, Majure, Aug. 19, 1988.
UMMZ 82896 (1) Elrod, H. H. Smith, 1 Sep. 1911.

18. *Medionidus acutissimus*
CMNH 61-8477 (3) The Forks, Texas, H. H. Smith 1910-11.
OSUM 29063 (3) Hwy. 23, Stansbery and Borror, 27 Oct. 1987.
UMMZ 98494 The Forks, Texas, H. H. Smith.
UMMZ 98495 Elrod, H. H. Smith, Sep. 1911.

19. *Megalonaias nervosa*
MMNS 2018 (3) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 2800 (1) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.

20. *Obliquaria reflexa*
FLMNH 197532 (1) Hwy. 82, Pierson and Puleo, 29 Sep. 1990.
FLMNH 197560 (1) Hwy. 23, M. Pierson, 6 July 1990.
FLMNH 197573 (8) Hwy. 2, Pierson and Hartfield, 29 Sep. 1991.
FLMNH 197579 (1) Hwy. 2, Pierson and Hartfield, 27 Sep. 1991.
FLMNH 197613 (11) Hwy. 2, Pierson and Hartfield, 27 Sep. 1991.
FLMNH 197681 (4) Hwy. 14, M. Pierson, 14 Nov. 1991.
FLMNH 197757 (1) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
FLMNH 197816 (2) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
FLMNH 244557 (1) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
MMNS 2794 (16) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.

21. *Obovaria jacksoniana*
CMNH 61-8421 (3) The Forks, Texas, H. H. Smith, 1910-11.
CMNH 61-8422 (4) Fayette, H. H. Smith, 1910-11.
MMNS 2088 (20) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 2791 (14) Hwy. 23, Hartfield, Jones, Majure, 19 Sep. 1988.
MMNS 4865 (4) Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.
UMMZ 54931 (5) Elrod, H. H. Smith, 1 Sep. 1911.
UMMZ 107504 (3) Fayette, H. H. Smith.
UMMZ 107505 (3) The Forks, Texas, H. H. Smith 1910-11.
UMMZ 107535 (6) Elrod, H. H. Smith, 1 Sep. 1911.
UMMZ 163838 (6) Elrod, H. H. Smith, 1 Sep. 1911.

22. *Obovaria unicolor*
CMNH 61-8418 (1) The Forks, Texas, H. H. Smith, 1910-11.
CMNH 61-8419 (2) Elrod, H. H. Smith, 1 Sep. 1911.
MMNS 2087 (15) Hwy. 23, Hartfield, Stewart, Williams, 12 Sep. 1984.
MMNS 2786 (9) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1984.
MMNS 4866 (8) Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.
MMNS 4913 (1) Hwy. 14, Hartfield, Williams, Stewart, 12 Sep. 1984.
UIMNH 14975 (2) Elrod, H. H. Smith, 1 Sep. 1911.
UMMZ 106250 (4) Elrod, H. H. Smith, 1 Sep. 1911.

23. *Plectomerus dombeyanus*
MMNS 2023 (1) Hwy 23, P. Hartfield *et al.*, 12 Sep. 1984.

24. *Pleurobema decisum*
CMNH 61-8267 (2) Fayette, H. H. Smith, 1910-11.
CMNH 61-8304 (3) Fayette, H. H. Smith, 1910-11.
MMNS 2016 (44) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 2796 (52) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.
MMNS 4911 (1) Hwy. 14, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 5144 (26) Hwy. 23, Hartfield, Stewart, Williams, 11 Sep. 1984.
OSUM 19146 (2) Hwy. 14, G. T. Watters, 28 July 1986.
OSUM 29054 (37) Hwy. 23, Stansbery and Borror, 27 Oct. 1987.
OSUM 29141 (3) Hwy. 23, G. T. Watters, 28 July 1986.
OSUM 45706 (2) Hwy. 82, W. and L. Starnes, 3 Sep. 1978.
OSUM 50231 (1) Brownville, Hwy. 21, L. M. Koch, 10 Oct. 1981.

25. *Pleurobema perovatum*
CMNH 61-8302 (10) The Forks, Texas, H. H. Smith, 1910-11.
CMNH 61-8303 (2) Fayette, H. H. Smith, 1910-11.
MMNS 2083 (4) Hwy. 23, Hartfield, Stewart, Williams, 12 Sep. 1984.
MMNS 2094 (1) Hwy. 14, Hartfield, Stewart, Williams, 12 Sep. 1984.
MMNS 2790 (6) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.
MMNS 4864 (1) Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.
OSUM 29055 (13) Hwy. 23, Stansbery and Borror, 27 Oct. 1987.
OSUM 29153 (1) Hwy. 2, G. T. Watters, 25 July 1986.
OSUM 50219 (1) Hwy. 82, L. M. Koch, 10 Oct. 1981.

26. *Pleurobema taitianum*
MMNS 2084 (1) downstream of Hwy 23, P. Hartfield *et al.*, 12 Sep. 1984.
van der Schalie (1981) noted Smith recorded *P. taitianum* from the Sipsey, but we were unable to find the specimen.

28. *Potamilus purpuratus*
MMNS 4902 (4) Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.
MMNS 4910 (1) Hwy. 14, Hartfield, Williams, Stewart, 12 Sep. 1984.

32. *Quadrula asperata*
CMNH 61-8229 (4) Fayette, H. H. Smith, 1910-11.
FLMNH 68812 (14) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 68813 (17) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 68817 (5) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 68828 (2) Elrod, H. H. Smith, 9 Sep. 1911.

FLMNH 68833 (2) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 68888 (3) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 68890 (5) Elrod, H. H. Smith, 8 July 1911.
MMNS 2017 (22) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 2795 (52) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.
MMNS 4862 (9) Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.
UMMZ 163842 Elrod, H. H. Smith, Sep. 1911.

33. *Quadrula metanevra*
CMNH 61-7225 (1) The Forks, Texas, Clapp Coll.

34. *Quadrula rumphiana*
ANSP 366812 Aliceville, Pickens Co., S. Ahlstedt, 1985.
ANSP 397246 A17368 Mantua, Greene Co., M. Pierson, 1991.
FLMNH 197533 Elrod, Pierson, 29 Sep. 1990.
FLMNH 197562 Hwy. 23, Pierson, 6 July 1990.
FLMNH 197580 Hwy. 2, Pierson, 27 Sep. 1991.
FLMNH 197682 Hwy 14, Pierson, 14 Nov. 1991.
FLMNH 197696 Hwy. 2, Pierson, 13 Aug. 1991.
FLMNH 197717 Hwy. 2, Pierson, 27 Sep. 1991.
FLMNH 197722 Mantua, Pierson, 20 Oct. 1991.
FLMNH 197760 Hwy. 23, Pierson, 26 Sep. 1991.
FLMNH 197804 Carpenter Creek, Pierson, 26 Sep. 1991.
FLMNH 197822 Hwy. 23, Pierson, 26 Sep. 1991.
MMNS 2020 (10) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 2793 (23) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.
MMNS 4581 (1) Sipsey River Greene County, 22 July 1991.
MMNS 4863 (13) Hwy. 23, Hartfield, Williams, Stewart, 11 Sep. 1984.

35. *Quadrula stapes*
MMNS 2085 (1) Hwy. 23, Hartfield, Stewart, Williams, 12 Sep. 1984.
OSUM 29049 (1) Hwy. 23, Stansbery *et al.*, 27 Oct. 1987.

36. *Strophitus subvexus*
CMNH 61-8380 (1) Fayette, H. H. Smith, 1910-11.
CMNH 61-8381 (6) The Forks, Texas, H. H. Smith, 1910-11.
MMNS 2012 Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
OSUM 50226 (1) Hwy. 21, L. M. Koch, 10 Oct. 1981.
UMMZ 74914 Fayette, H. H. Smith.
UMMZ 74915 Fayette, H. H. Smith.
UMMZ 74925 The Forks, Texas, H. H. Smith.
UMMZ 74935 The Forks, Texas, H. H. Smith.

37. *Toxolasma parvus*
CMNH 61-8456 (1) Fayette, H. H. Smith, 1910-11.
CMNH 61-8457 (4) The Forks, Texas, H. H. Smith, 1910-11.
CMNH 61-8458 (2) Ballard Cr., H. H. Smith, 1910-11.

38. *Tritogonia verrucosa*
CMNH 61-7221 (5) Fayette, H. H. Smith, 1910-11.
CMNH 61-7222 (2) The Forks, Texas, H. H. Smith, 1910-11.
CMNH 61-8254 (3) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 68085 (13) Elrod, H. H. Smith, 1 Sep. 1911.
FLMNH 197534 (2) Hwy. 82, Pierson and Puleo, 29 Sep. 1990.
FLMNH 197561 (1) Hwy. 23, M. Pierson, 6 July 1990.
FLMNH 197610 (15) Hwy. 2, Pierson and Hartfield, 21 Sep. 1991.
FLMNH 197674 (3) Hwy. 14, Pierson, 14 Nov. 1991.
FLMNH 197695 (1) Hwy. 2, Pierson and Puleo, 13 Aug. 1991.
FLMNH 197750 (5) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
FLMNH 197796 (2) Hwy. 2, Pierson and Hartfield, 26 Sep. 1991.
FLMNH 197823 (2) Hwy. 23, Pierson and Hartfield, 26 Sep. 1991.
FLMNH 197861 (9) Hwy. 2, Pierson and Puleo, 20 Oct. 1991.
FLMNH 207958 (6) Hwy. 2, Pierson and Hartfield, 27 Sep. 1991.
FLMNH 245962 (3) Hwy. 2, M. Pierson, 27 Sep. 1991.
MCZ 64045 (6) Elrod, H. H. Smith, 8 July 1911.
MCZ 91250 (4) Elrod, H. H. Smith, 1 Sep. 1911.
MMNS 2021 (14) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 2782 (12) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.
MMNS 4895 (2) Hwy. 23, Hartfield, Stewart, Williams, 11 Sep. 1984.

40. *Uniomerus tetralasmus*
CMNH 61-8366 (2) Fayette, H. H. Smith, 1910-11.

42. *Villosa lienosa*
CMNH 61-8506 (4) Elrod, H. H. Smith, 1 Sep. 1911.
CMNH 61-8507 (12) Fayette, H. H. Smith, 1910-11.
CMNH 61-8508 (13) The Forks, Texas, H. H. Smith, 1910-11.
CMNH 61-8509 (5) Ballard Cr., H. H. Smith, 1910-11.
MMNS 2015 (9) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS2785 (3) Hwy. 23, Hartfield, Williams, Stewart, 19 Aug. 1988.
MMNS 2024 (55) Hwy. 23, Hartfield, Williams, Stewart, 12 Sep. 1984.
MMNS 2788 (17) Hwy. 23, Hartfield, Jones, Majure, 19 Aug. 1988.
MMNS 4632 (2) Sipsey River Pickens County, Clay Moore, 1 Sep. 1990.
MMNS 4796 (4) Hwy. 23, Hartfield, Stewart, Williams, 11 Sep. 1984.
UMMZ 30931 The Forks, Texas, H. H. Smith.
UMMZ 62332 Fayette, H. H. Smith.
UMMZ 67528 Elrod, H. H. Smith, 8 July 1911.
UMMZ 86196 Fayette, H. H. Smith.
UMMZ 86208 Elrod, H. H. Smith, Sep. 1911.
UMMZ 163835 Elrod, H. H. Smith, Sep. 1911.

43. *Villosa vibex*
CMNH 61-8480 (1) Fayette, H. H. Smith, 1910-11.
CMNH 61-8481 (4) The Forks, Texas, H. H. Smith, 1910-11.
UMMZ 62355 The Forks, Texas, H. H. Smith.
UMMZ 89056 The Forks, Texas, H. H. Smith.
UMMZ8057 Fayette, H. H. Smith.
UMMZ 89062 Elrod, H. H. Smith, Sep. 1911.

Reanalysis of functional design of *Nautilus* locomotory and respiratory systems

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Abstract: Morphology of the mantle cavity complex and microanatomy of the funnel, collar folds, and retractor muscles were analyzed from 5 specimens of *Nautilus pompilius* Linnaeus, 1758 to model how these structures perform during respiration and locomotion. In addition to well-known cephalopodium retractors, a pair of short nuchal retractors was found, which attach the collar folds and the wings to the shell. Microstructure of the cephalopodium retractors and the funnel exhibit a typically molluscan pattern of tightly-packed three-dimensional arrangement of muscle fibers. Muscular arrangement in the wings and the nuchal retractors is simpler, consisting of two groups of muscles (longitudinal and transverse) and one group of muscle (longitudinal), correspondingly. Functional conflict was revealed between respiratory and locomotory systems in *Nautilus*. During jetting, the strong flows produced by the piston-like movements of the head would displace the gills from their working position, pressing them against the ventral wall of the mantle. Flexible support of the gills prohibited intensification of the ventilatory flows and did not allow jet propulsion to become a powerful means of locomotion in *Nautilus*. Apparently, the evolutionary answer of *Nautilus* to the dilemma "to breathe or to move," was development of a "quiet respiration pattern" that combined breathing with slow sustained swimming.

Key Words: *Nautilus*, morphology, muscles, jet swimming, respiration

Five or six living species of genus *Nautilus* represent the last remnants of an ancient phyletic line that extends back 300-500 My ago to the beginning of cephalopod evolution. *Nautilus* retain a remarkable number of archaic features in their shells and soft body structures and are often referred to as living fossils. Their organization may be considered a starting point in the comparative and phylogenetic research on cephalopods, similar to the lamprey in the evolution of fishes.

Locomotion and respiration in cephalopods are accomplished by muscular actions; the mantle cavity is used to contain water to produce jet strokes and to ventilate the gills. The modes of locomotion and respiration of *Nautilus* are particularly interesting. As in other cephalopods, *Nautilus* breathes using gills and moves by taking water into the mantle cavity and jetting it out under pressure through the funnel. However, the weak mantle musculature cannot act in move water the same way it does in coleoid cephalopods. The presence of a rigid external shell that accommodates the soft body places considerable constraints on *Nautilus* locomotion and ventilation patterns.

The soft body of *Nautilus* is markedly curved dorsally, strictly corresponding to the shape of the living chamber of the shell. It consists of the head, the hood, a large muscular funnel, the mantle, and the visceral sac with siphuncle (Fig. 1). The visceral sac is completely covered by the mantle, which, in turn, is closely applied to the inner surface of the shell. Anteriorly, the mantle projects into a thin muscular fold (pallial fold) that confines the mantle cavity around the visceral sac. Posteriorly, the mantle forms the transparent membranous integument of the visceral sac and siphuncle (Owen, 1832; Willey, 1902). The outer surface of the mantle is lined with shell epithelium that produces shell.

The mantle cavity is rather narrow laterally and more spacious ventrally. The muscular system of the mantle cavity consists of a pair of cephalopodium retractors and the funnel with its associated structures. The cephalopodium retractors are wide powerful ribbon-like muscles that extend from the buccal part of the head to the lateral sides of the visceral sac where they attach to the shell. The sites of attachment are visible on the surface of the visceral sac (Fig. 1).

The funnel consists of a triangular muscular sheet originating below the head. Its folds are wrapped around each other to make a tube tapering beyond the shell edge. Posteriorly, the funnel fastens to the visceral sac by narrow retractor muscles (funnel retractors). The collar is a struc-

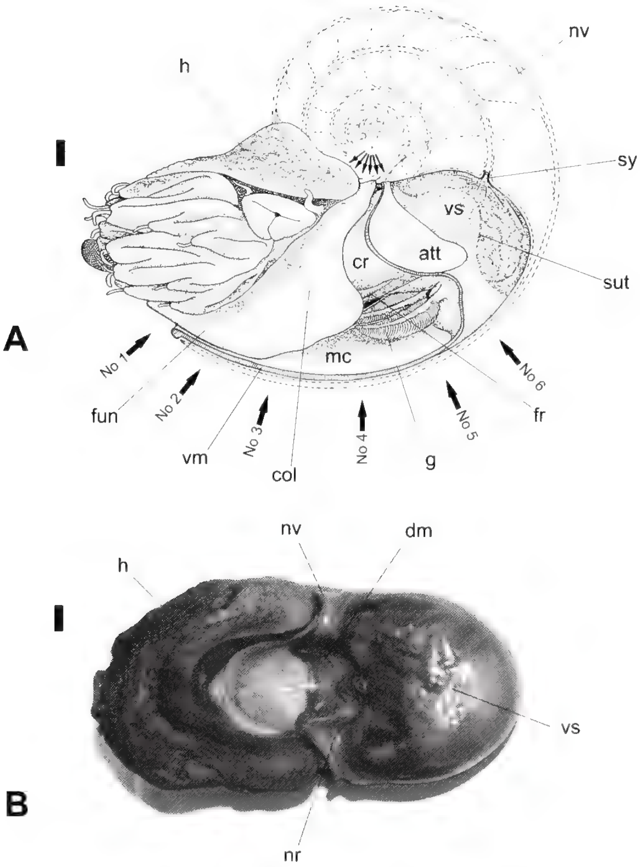

Fig. 1. Morphology of the soft body of *Nautilus pompilius*. A. Lateral view (lateral wall of the mantle with the left anterior gill cut away; the shell contour is shown by a dashed line). Bold arrows with numbers indicate the planes of corresponding cross-sections; scale bar = 10 mm. B. Dorsal view (photo); scale bar = 10 mm. Abbreviations: att, attachment site of the cephalopodium retractor; col, collar; cr, cephalopodium retractor; dm, dorsal lobe of the mantle; fr, funnel retractor; fun, funnel; g, gills; h, hood; mc, mantle cavity; nr, attachment site of the nuchal retractor; nv, nuchal valve; sut, suture line of the last septum; sy, siphuncle; vm, ventral lobe of the mantle (pallial fold); vs, visceral sac.

ture associated with the funnel and consists of a pair of muscular folds that project backward from the lateral sides of the cephalic sheath and adhere to the mantle. The collar folds are narrow on the dorsal side, gradually widen ventrally, and pass into the funnel without distinct borders. On the dorsal side they form muscular flaps, the nuchal valves, which play an important role in pumping water into the mantle cavity during the ventilation cycle. The free distal margins of the collar and funnel are fused into wings - thin muscular flaps that in life are always active (Wells, 1988). Together, the collar folds and the funnel form the collar pockets - a pair of spacious cavities on the lateral sides of the head (Naef, 1923).

Experimental studies on *Nautilus* respiration and swimming began in the 1960s when adequate techniques for aquarium maintenance of this animal were developed. Bidder (1962) noted that the mantle wall in *Nautilus* does not take part in swimming as it does in coleoid cephalopods. Zuev (1967) supposed that the processes of taking water into the mantle cavity and jetting it out are not functionally separated in *Nautilus* and are performed simultaneously. Direct aquarium observations revealed two principal swimming modes of *Nautilus*: gentle respiratory movement and active jet-propelled swimming.

Respiratory flows and the ventilation cycle of *Nautilus* were thoroughly described by Packard *et al.* (1980), Wells and Wells (1985), and Wells (1988). According to these authors, respiratory flows in *Nautilus* are generated by continuous coordinated undulation of the wings, the collar folds (including the nuchal valves), and the funnel folds. At the beginning of the ventilation cycle, the nuchal valves behind the hood pull down inside the mantle cavity, pumping the water into spacious collar pockets. Then the nuchal valves close, and the water trapped in the collar pockets is forced down the gills by an undulatory movement of the wings and collar folds. Passing through the gills, the water is jetted out through the funnel by undulation of the wings and contraction of the funnel lobes. Because the head and the hood remain almost still during the ventilation cycle, the volume of the ventral mantle cavity changes only slightly. The ventilation stroke volume is determined largely by the water expelled from the collar pockets, from 4% to 16% of the total volume of the mantle cavity (Johansen *et al.*, 1978; Wells, 1988). Respiratory flow produced from the funnel is sufficient to drive an animal slowly backward at the speed of 5-10 cm/s (Packard *et al.*, 1980).

The gills (two on each side) play an important role in directing the ventilatory flows. They lie along the exits of the collar pockets, and their soft lamellae act as valves preventing any backflow during the respiratory cycle. According to Wells (1988), the gills divide the mantle cavity of *Nautilus* into three functional chambers: two lateral, prebranchial (collar pockets) and the third ventral, postbranchial (the funnel cavity). In contrast to coleoid cephalopods, in *Nautilus* the gills have no longitudinal membranous attachment to the mantle and hang freely into the mantle cavity. Each gill is supported in a horizontal position by a flexible axial rib of connective tissue running along its dorsal side (Naef, 1923).

During fast swimming, *Nautilus* produces jet strokes by rhythmic piston-like movements of the cephalic and pedal parts of the body within the living chamber (Bidder, 1962; Packard *et al.*, 1980). Such pumping movement is accomplished by powerful cephalopodium retractors. The jet propulsion cycle begins with outward elastic re-extension of the cephalic and pedal parts of the body when the mantle cavity expands and fills the water. Then the collar folds and the nuchal valves close the slit between the head and the mantle, sealing the mantle cavity, and the cephalopodium retractors contract, pulling the body inside and building up pressure in the mantle cavity. The water is jetted out through the funnel. The funnel controls the direction and power of thrust by adjusting the shape and size of its nozzle. Using active jetting, an adult animal may accelerate up to 25 cm/s (Chamberlain and Westermann, 1976; Ward *et al.*, 1977). However, it could not keep such a speed for more than a few minutes and then had to rest and breathe heavily (Wells, 1988). When the animal is breathing deeply after a period of activity, its funnel is wide open, minimizing the propulsive output of the jet to almost zero values. Apparently, in natural conditions *Nautilus* alternates prolonged periods of slow swimming or drifting with a few minutes of activity, as it does in aquarium (Zann, 1984).

Comparison of swimming and breathing systems in *Nautilus* reveals a considerable number of morphological structures - mantle cavity, cephalopodium retractors, funnel, collar folds, wings, etc. - that take part in both functions. It is still unclear how these two systems interplay and balance each other. Wells (1988) noted that during jetting the frequency of strokes may double but oxygen extraction rate sharply declines from 9-12% to 4-7%. This indicates a conflict between swimming and breathing mechanisms in *Nautilus*. Because the musculature is primarily responsible for creating respiratory flow and jet thrust, analysis and functional interpretation of its morphology and histology may help to understand the functional design of locomotory and respiratory systems in this animal.

This paper provides a morphological and histological description of the soft body and musculature of *Nautilus* and suggests mechanisms of their performance during swimming and breathing.

MATERIAL AND METHODS

Four specimens of *Nautilus pompilius* Linnaeus, 1758 were purchased through the Coral Shop of 'Kabukshiki Kaisha Monako Kenkyusho' in Tokyo, Japan. The specimens were reported to have been trapped off the Pacific coast of Mindanao, Southern Philippines, in July 1998, at depths of about 200 m. All four specimens were immature males. They were frozen and brought to Moscow and after thawing were preserved in 4% buffered formalin. Two other males (soft bodies only) were obtained from the collection of the Zoological Museum of Moscow State University (registration number J-379). These specimens were caught in the Coral Sea (the Great Barrier Reef) in 1975. Shell diameter, total weight, soft body weight, sex, and stage of maturity were measured, when possible, for each specimen (Table 1).

To study gross morphology and internal structure of *Nautilus*, the soft bodies of three immature specimens were cross-sectioned at 6 planes (Fig. 1). As the body of *Nautilus* is curved, the planes of sections were not parallel to each other but radiate from the umbilical region of the shell. The total cross-sections of the soft body were made using the following procedure: each specimen was extracted from its shell, washed in fresh water, then frozen at -24ºC for 4-6 hours. After complete freezing they were cross-sectioned manually (by hand) with a microtome knife fixed in a handle. With some experience, in this way I could obtain cross-sections that had a thickness of approximately 0.3 to 1.0 mm. The cross-sections were put in a glass dish with water and drawn using a SZH-10 Olympus zoom microscope with a drawing tube.

The microstructures of funnel, wings, and retractors of *Nautilus* was studied using histological cross-sections. Four samples of muscular tissues were cut out from one formalin-preserved museum specimen (J-379): (1) a fragment of the left cephalopodium retractor taken approximately 5 mm from the site of its attachment to the shell; (2) a fragment from the ventro-lateral wall of the funnel in its middle part; (3) a fragment of the wing from the left wing just behind the eye; 4) a fragment from the retractor muscle originating behind the nuchal valves. The tissues were dehydrated through a graded series of ethanols, cleared in xylene, and embedded in paraffin. All fragments excluding the wing were serially cut in a transverse plane at 7-10 μm with a rotary microtome. The sample of wing tissue was cut in the

Table 1. Morphometric data on studied specimens of *Nautilus pompilius*. Registration numbers belong to the Moscow Zoological Museum.

No.	Registration No.	Locality	Sex	Maturity	Shell diameter (mm)	Weight total (g)	Soft body weight (g)
1	-	Mindanao	male	immature	108	184	101
2	-	Mindanao	male	immature	116	198	107
3	-	Mindanao	male	immature	99 168	97	
4	J-372	Mindanao	male	immature	114	201	-
5	J-379	Coral Sea	male	immature	- -		170
6	J-379	Coral Sea	male	mature	- -		640

frontal plane from the proximal base to the distal margin. Two staining procedures were used: (1) Mallory's tricolor technique and (2) Azan technique (Romeis, 1953). Both stains show strong contrast between muscle and connective tissues. The sections were examined in transmitted light under a Nikon Optiphot-2 light microscope.

RESULTS

Gross morphology of the soft body

Morphology of the soft body of *Nautilus* has been described in considerable detail in a number of classic works (Owen, 1832; Griffin, 1900; Willey, 1902; Naef, 1923). However, my study revealed that some features of its musculature differ from those reported previously. I found a pair of short and powerful muscles that originate from the nuchal valves of the collar folds and extend backward to the dorsal wall of the living chamber of the shell. These muscles are covered by the dorsal mantle lobe and are hardly discernible on the intact *Nautilus* body but are obvious in the cross-sections. In the sections they look like thick crescent-like flaps that lie in the umbilical regions on the dorsal side of the visceral sac and fuse with it by their inner margins (Fig. 4, nuchal retractor, nr). The dorsal mantle cavity surrounds them, forming an almost complete tube around each muscle. The ventral side of these muscles is concave, covered by some apparently cartilaginous substance bearing tiny longitudinal wrinkles. The muscle attachment sites are crescent-like, situated in the umbilical region on the surface of the preceding whorl (Fig. 1B). At the sites of attachment these muscles are partly fused with the cephalopodium retractors. I called these muscles the "nuchal retractors" as they apparently serve to attach the wings and nuchal valves to the shell.

Internal structure of the soft body

The cross-section through the buccal region at the level of the eyes (Fig. 2A) shows the relationship between the head and funnel, and the origin of the cephalopodium retractors. The anterior free part of the funnel (funnel nozzle) is situated on the ventral side of the head in a deep depression formed by the tentacle sheaths. The funnel nozzle is muscular, roughly rectangular in cross-section,

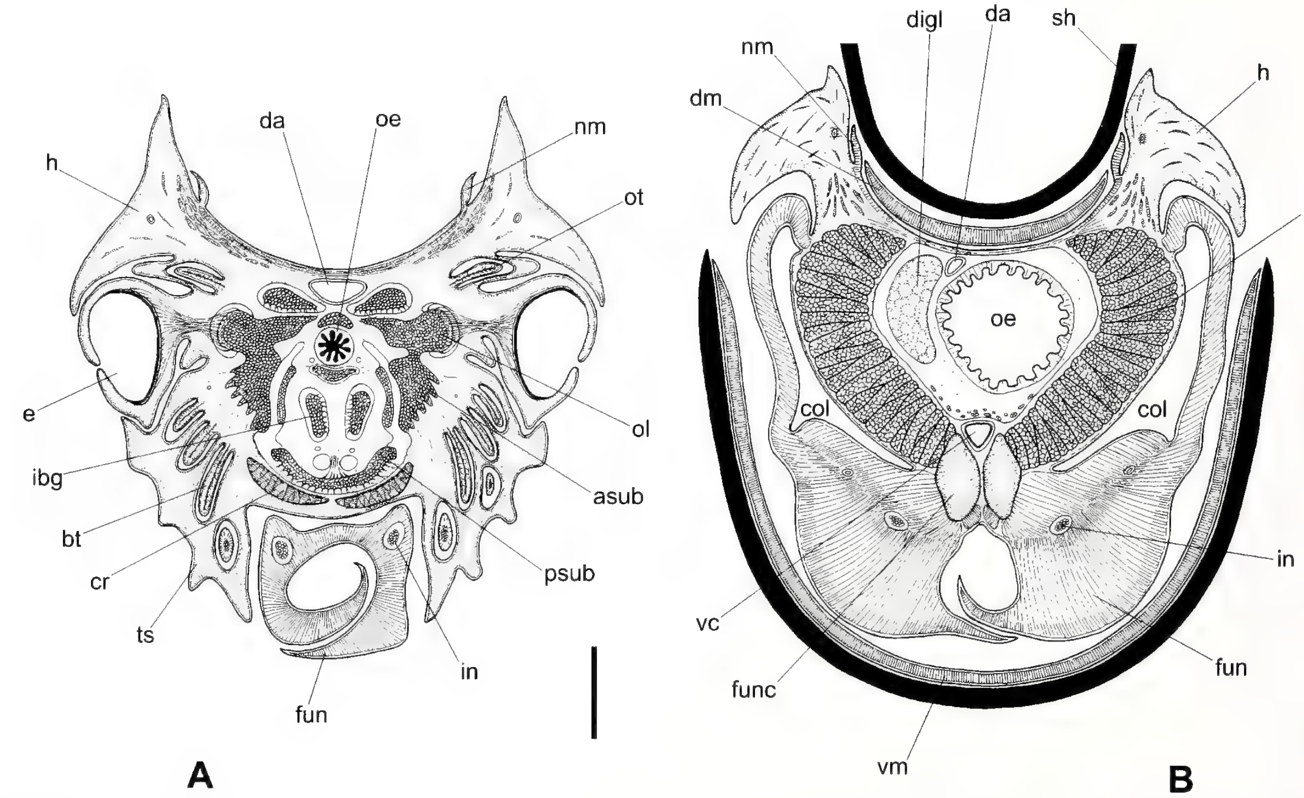

Fig. 2. Schematic cross-sections of *Nautilus* soft body; scale bar = 10 mm. A. Section 1, through the eyes. B. Section 2, from the posterior part of the hood to the middle part of the funnel. The position of the sections is indicated on Fig. 1. Abbreviations: asub, anterior subesophageal nerve mass; bt, bases of the tentacles; col, collar pockets; cr, cephalopodium retractor; da, dorsal aorta; digl, digestive gland; dm, dorsal lobe of the mantle; e, eye; fun, funnel; func, funnel cartilage; h, hood; ibg, inferior buccal ganglion; in, infundibular nerve; nm, nuchal membrane; oe, esophagus; ol, optic lobe; ot, ophthalmic tentacles; psub, posterior subesophageal nerve mass; sh, shell; ts, tentacle sheaths; vc, vena cava; vm, ventral lobe of the mantle.

with a pair of large infundibular nerves passing along its dorsal angles. The head and the hood (or the head sheath, after Naef, 1923), are composed mainly of connective tissue. The hood also contains dispersed muscle fibers and a muscular nuchal membrane on its dorsal side. The cephalopodium retractor muscles originate at this level on the ventral side of the head just below the brain. They form a pair of small muscular bands enclosed by surrounding connective tissue and are richly enervated from the posterior subesophageal mass of the brain. As in other cephalopods, the brain in *Nautilus* is arranged around the esophagus and consists of supraesophageal cord, two subesophageal nerve masses, and a magnocellular lobe at the sides (Young, 1988). A characteristic feature of the brain of *Nautilus* is that all its parts are widely separated from one another. There is no cephalic cartilage around them.

The section through the posterior part of the hood and middle of the funnel (Fig. 2B) illustrates the relationship of the funnel with the collar and visceral sac. At this level the ventral part of the soft body is protected by the shell, lined inside by the mantle. On the dorsal side, the preceding whorl of the shell occupies a concavity in the hood and is lined by the dorsal lobe of the mantle. On the lateral sides a pair of muscular collar folds appear, originating from the funnel and attaching to the visceral sac. The collar folds confine two cavities on the lateral sides of the visceral sac, the collar pockets. The funnel consists of two thick muscular lobes separated along the mid-line by a strip of connective tissue and a pair of transverse muscles. The latter apparently may affect the shape and size of the funnel. The ventral margins of the funnel overlap to form the funnel tube. The funnel attaches to the visceral sac through the funnel cartilage, which at this level consists of two laterally compressed lobes. The funnel cartilage also provides support for the robust cephalopodium retractors, which form the thick muscular lateral walls of the visceral sac. The inner sides of the funnel cartilage form a longitudinal depression that contains the vena cava. The visceral sac contains the large crop, digestive gland, and dorsal aorta.

At the level of the nuchal valves and posterior part of the funnel (Fig. 3A), the collar pockets become more spacious, expanding both dorsally and ventrally. The collar folds attach to the dorsal sides of the visceral sac where they form prominent muscular ridges, the nuchal valves. The cephalopodium retractors compose the thick muscular ventro-lateral walls of the visceral sac and almost meet each other on its ventral side. The vena cava is situated in a V-shaped longitudinal slit formed by converging edges of

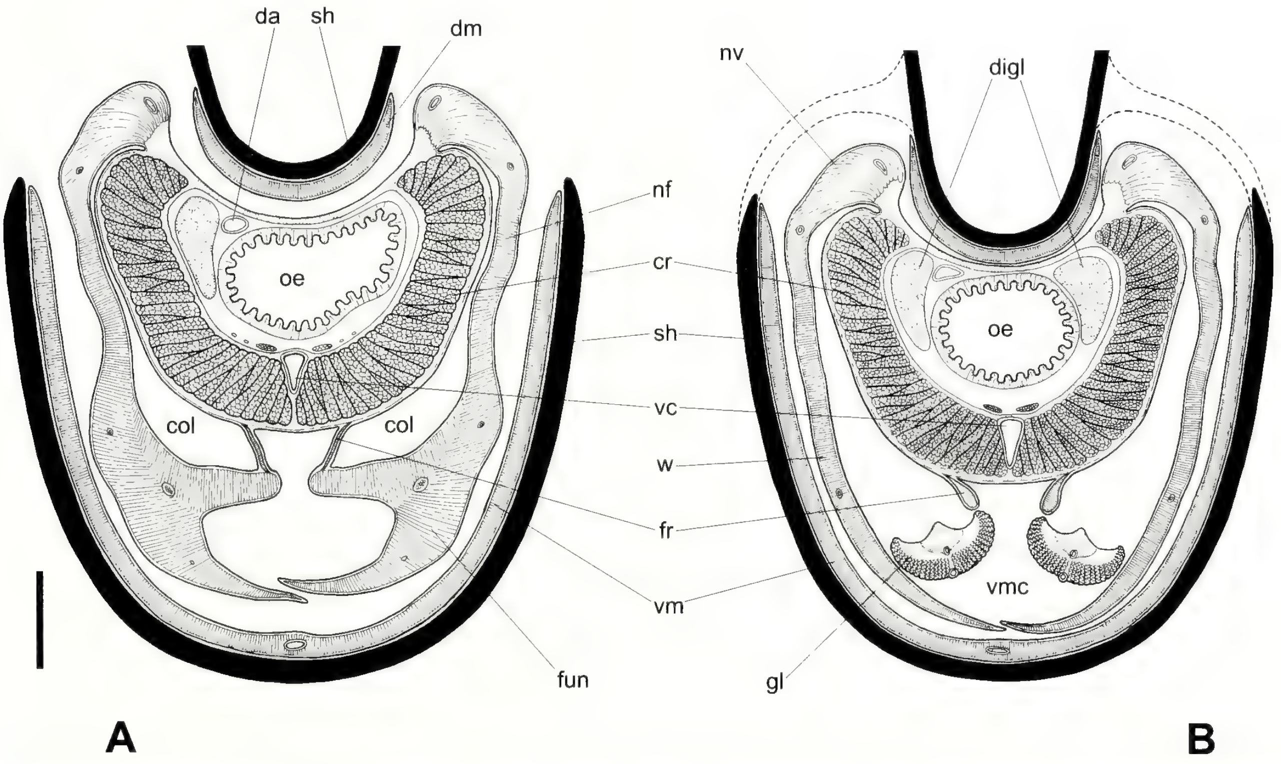

Fig. 3. Schematic cross-sections of *Nautilus* soft body; scale bar = 10 mm. A. Section 3, from the nuchal valves to the posterior part of the funnel; B. Section 4, through the nuchal valve and funnel wings. Abbreviations: col, collar pockets; cr, cephalopodium retractor; da, dorsal aorta; digl, digestive gland; dm, dorsal lobe of the mantle; fr, funnel retractors; fun, funnel; gl, gills; nf, collar fold; nv, nuchal valves; oe, esophagus; sh, shell; vc, vena cava; vm, ventral lobe of the mantle; vmc, ventral mantle cavity; w, wing.

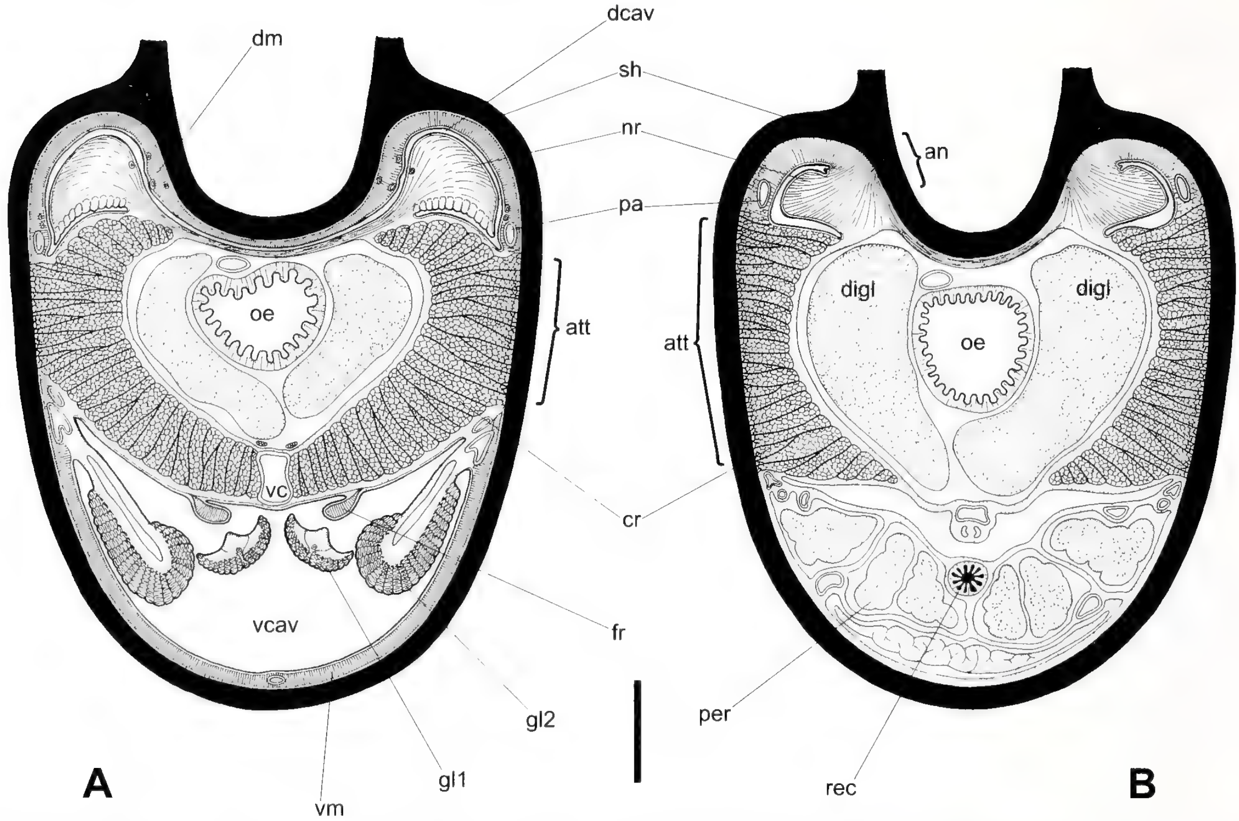

Fig. 4. Schematic cross-sections of *Nautilus* soft body; scale bar = 10 mm. A. Section 5, at the level of the anterior gill attachments. B. Section 6, at the level of the retractor muscles attachment site. Abbreviations: an, attachment of nuchal retractor; att, attachment site of cephalopodium retractor; cr, cephalopodium retractor; dcav, dorsal mantle cavity; digl, digestive gland; dm, dorsal lobe of the mantle; fr, funnel retractor; gl1, upper gill; gl2, lower gill; nr, nuchal retractor; oe, esophagus; pa, pallial artery; per, pericardium appendages; rec, rectum; sh, shell; vc, vena cava; vcav, ventral mantle cavity; vm, ventral lobe of the mantle.

cephalopodium retractors. The visceral sac is occupied mainly by the large crop. The funnel becomes thinner posteriorly. Its lobes are widely separated along the mid-line. The funnel cartilage is absent at this level. Attachment of the funnel to the visceral sac occurs through the funnel retractors that originate as posterior extensions of the funnel dorsal walls. The funnel retractors adhere to the connective matrix on the ventral side of the visceral sac.

The section passing through the nuchal valve and the wings (Fig. 3B) is important in understanding the ventilatory mechanism of *Nautilus*. At this level the shell almost completely surrounds the soft body, leaving small apertures in the umbilical regions where the water enters the mantle cavity. Posterior extensions of the collar and funnel are fused together to form the wings, a pair of thin, muscular folds that generate ventilatory flows toward the gills. Dorsal parts of the wings form muscular flaps, the nuchal valves, that correspond in size to the umbilical apertures of the shell. The collar pockets greatly increase in volume. They are narrow on the dorsal side, then gradually widen ventrally toward the gills. On the ventral side of the visceral sac there is a pair of muscular ridges, the funnel retractors. The gills are supported by fleshy axial ribs in their position right along the outlets of the collar pockets.

The section at the anterior part of the cephalopodium retractor attachment sites (Fig. 4A) reveals the relationship between the cephalopodium retractors and the shell. At this level, the cephalopodium retractors attach to the shell by their lateral parts whereas the dorso-lateral and ventral parts are still free, encircling the visceral sac. The sites of attachment divide the mantle cavity into two parts: a spacious ventral and a narrow dorsal part. The ventral part of the mantle cavity contains the gills that hang freely from the corners between the cephalopodium retractors and the ventral wall of the mantle. The dorsal mantle cavity is of special interest as its structure has never been described before. It is a narrow slit-like space between the dorsal mantle lobe and the visceral sac. Posterior extensions of the nuchal valves are present at this level as two muscular nuchal retractors lying in the umbilical parts of the dorsal mantle cavity. They are thick and crescent-like in cross-section, attaching to the visceral sac by their inner sides.

The structure of the visceral sac remains generally the same. The vena cava shifts to the ventral surface of the visceral sac, dividing the cephalopodium retractors completely.

At the posterior part of cephalopodium retractor attachment sites (Fig. 4B), the muscles entirely cover the lateral and dorsal surface of the soft body except for the central region of the dorsal concavity. The ventral part of the body, on the contrary, is not muscular and contains the pericardial appendages and the rectum. At this level the mantle cavity remains on the dorsal side only as two small semicircular cavities surrounding the nuchal retractors. The cephalopodium retractors attach to the lateral walls of the living chamber while the nuchal retractors attach to its umbilical (dorso-lateral) parts, on both sides of the preceding whorl of the shell. The attachment sites of the cephalopodium and nuchal retractors are fused near the mantle pallial artery. The ventral margins of the cephalopodium retractors are connected by the membrane that comprises the vena cava and divides the visceral sac from the pallio-visceral complex.

Histology of the cephalopodium retractors

Three kinds of muscle fibers compose the cephalopodium retractors: longitudinal, transverse, and radial (Fig. 5). Longitudinal fibers are the most abundant in the cephalopodium retractors, making up the bulk of their volume. On the inner side of the retractors, facing the cavity of the visceral sac, there is a thick layer of transverse muscles covered inside by a pellicle of connective tissue (Fig. 5C). Numerous trabeculae of radial muscle fibers originate from the inner layer of the transverse muscle and extend toward the outer surface of the retractors (Fig. 5A, B). These trabeculae branch toward the outer surface of the cephalopodium retractor, dividing the surrounding longitudinal muscle into narrow segments. In the peripheral zone of the cephalopodium retractor, radial trabeculae penetrate a thick layer of fibrous connective tissue lying just outside the mass of longitudinal muscle and finally insert themselves on an outer layer of transverse muscle (Fig. 5A). Covering the outer transverse muscle is a tunic composed of two layers of fibrous connective tissue, the outer dense and the inner loose layer. The outer layer of the tunic is covered in turn by a simple columnar epithelium. Scattered throughout the mass of longitudinal muscle are small patches of vacuolated connective tissue that are usually attached to the radial trabeculae (Fig. 5B).

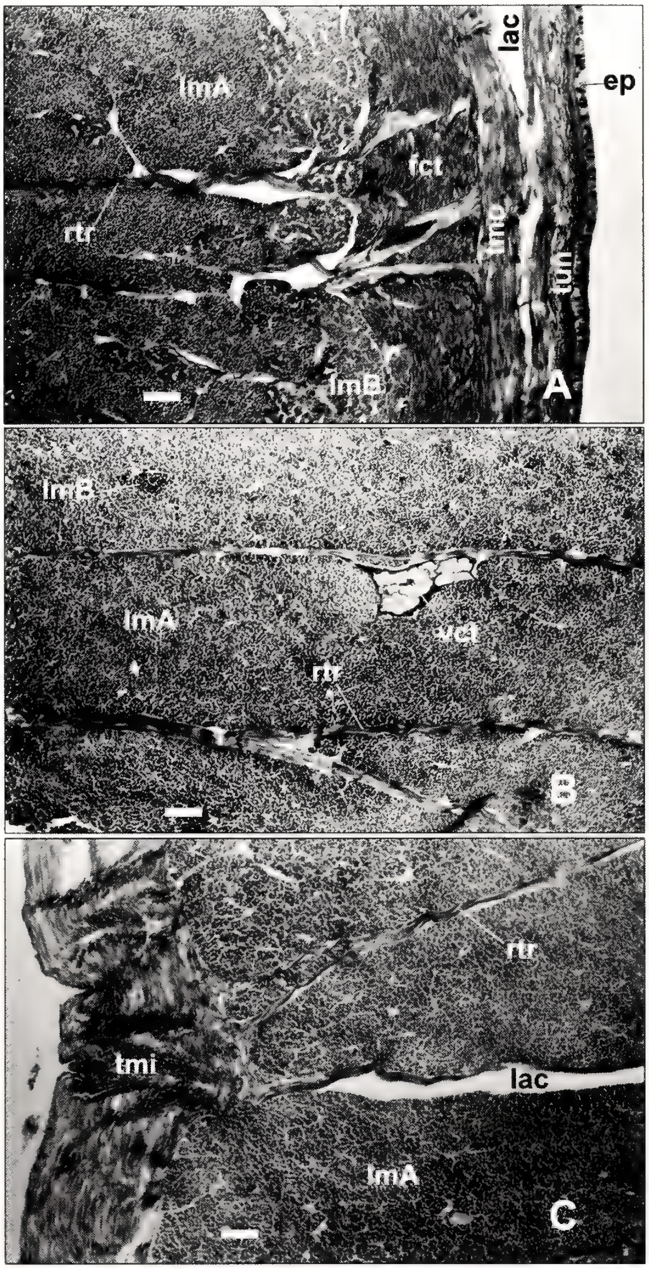

Fig. 5. Micrographs of a transverse section of the cephalopodium retractor of *Nautilus pompilius* (the outer side of the retractor muscle is on the right and the inner side is on the left). A. Outer lateral margin of the retractor; scale bar = 100 µm. B. Central part of the retractor; scale bar = 100 µm. C. Inner margin of the retractor; scale bar = 100 µm. Abbreviations: ep, epithelium; fct, layer of fibrous connective tissue; lac, hemolymph lacuna; lmA, longitudinal muscle of the first type (type A); lmB, longitudinal muscle of the second type (type B); rtr, trabeculae of radial muscle; tmi, inner layer of transverse muscle; tmo,outer layer of transverse muscle; tun, tunic of connective tissue; vct, vacuolated connective tissue.

Two morphological types of fibers stained differently with Azan were found within longitudinal muscle of cephalopodium retractors. The fibers of the first type were narrow, 2-4 µm in cross-sections, and stained in different shades of bluish-purple whereas fibers of the second type were somewhat wider, 4-8 µm in cross-section, and stained in reddish-purple. The fibers of both types were distributed separately, the first type of fibers comprised about 90% of longitudinal muscle and made up the bulk of the retractor, whereas the fibers of the second type comprised less than 10% and formed a narrow irregular layer in the peripheral zone of the retractor adjacent to the layer of fibrous connective tissue (Fig. 5A). Small compact groups of the second fiber type were also found scattered throughout the muscular mass of the fibers of the first type (Fig. 5B). Distribution of hemolymph lacunae was different between the two different types of fibers. There were a few lacunae in the core of the cephalopodium retractor composed by the first fiber type (Fig. 5A). In contrast, the peripheral layer of the retractor composed by the fibers of the second type was richly supplied by hemolymph lacunae.

Histology of the funnel

The funnel folds are composed of two muscular layers: the inner and the outer layer, separated by a thick intermediate zone of fibrous connective tissue (Fig. 6). Simple columnar epithelium with underlying collagen tunic covers both the outer and inner surfaces of the funnel. Similarly to the cephalopodium retractors, the funnel tunic consists of two layers of fibrous connective tissue. On the outer side of the funnel, incorporated with the inner loose tunic collagen layer, there is a row of bundles of longitudinal muscle fibers (Fig. 6A). Beneath the longitudinal bundles there is a layer of transverse muscle that is penetrated here and there by connective tissue and trabeculae of radial muscle fibers. Underlying the transverse muscle there is a thick layer of differently oriented oblique muscle fibers, separated into narrow bundles by numerous trabeculae of radial muscle and connective tissue (Fig. 6A). Thus, the outer muscular layer in the funnel wall is composed of four types of muscles: longitudinal, transverse, oblique, and radial, the oblique muscle being the most developed.

The intermediate zone of the funnel wall is occupied by connective tissue filled with twisted collagen fibers oriented in all directions (Fig. 6B). Muscles are represented by widely spaced trabeculae of radial fibers connecting the outer and the inner muscular layers. Hemolymph lacunae are almost absent in this zone.

The inner muscular layer of the funnel is less developed than the outer one. It consists of oblique muscle fibers separated into bundles of irregular shape by connective pellicle and hemolymph lacunae (Fig. 6C). Some lacunae in this layer have walls formed by surrounding connective tissue and therefore they may be considered as true vessels. The thickness of the inner muscular layer is 60-80% of that of the outer one. Collagen tunic on the inner surface of the funnel is half as thick as the tunic on the outer side of the funnel. Compared to the cephalopodium retractors, the musculature in the funnel is more diversified and complexly arranged, and the connective tissue in the funnel is much more developed. However, all muscle fibers were morphologically similar and stained in the same reddish-brown color. Different morphological types of muscle fibers, as seen in the cephalopodium retractors, were not found in the funnel.

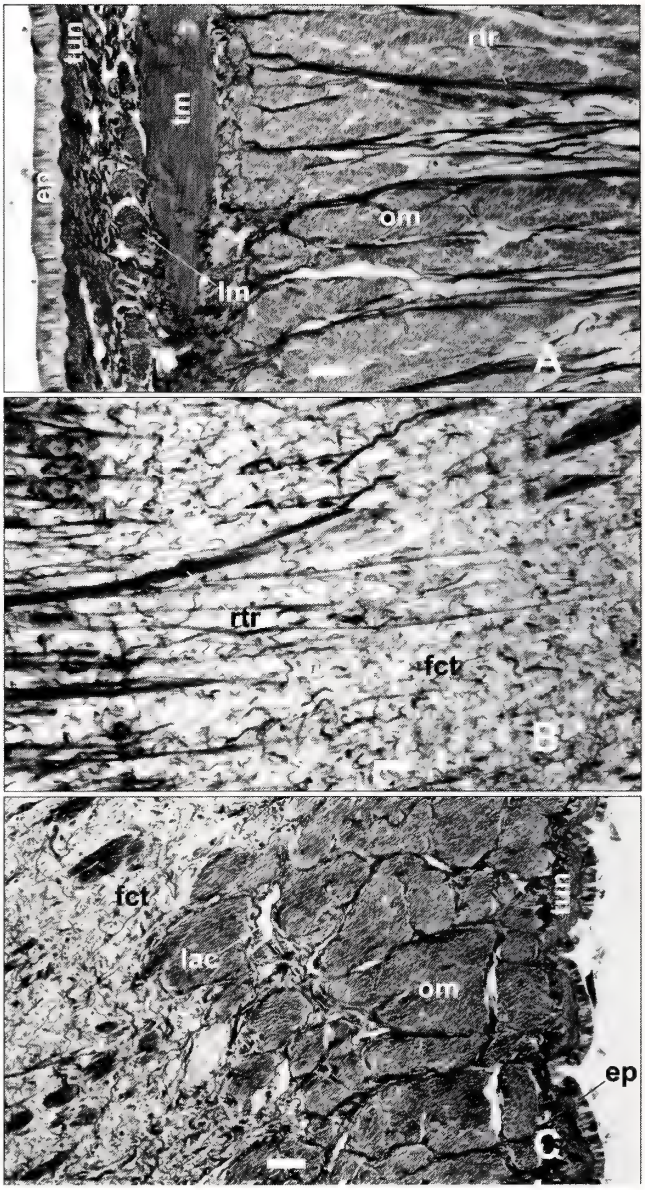

Fig. 6. Micrographs of a transverse section of the ventro-lateral wall of the funnel of *Nautilus pompilius* (the outer side of the funnel wall is on the left and the inner side is on the right). A. Outer part of the wall; scale bar = 100 μm. B. Middle part of the wall; scale bar = 100 μm. C. Inner part of the wall; scale bar = 100 μm. Abbreviations: ep, epithelium; fct, fibrous connective tissue; lac, hemolymph lacuna; lm, bundles of longitudinal muscles; om, oblique muscle; rtr, trabeculae of radial muscle; tm, layer of transverse muscle; tun, tunic of connective tissue.

Histology of the wings

The wings are composed of bundles of muscles associated with a highly developed network of hemolymph

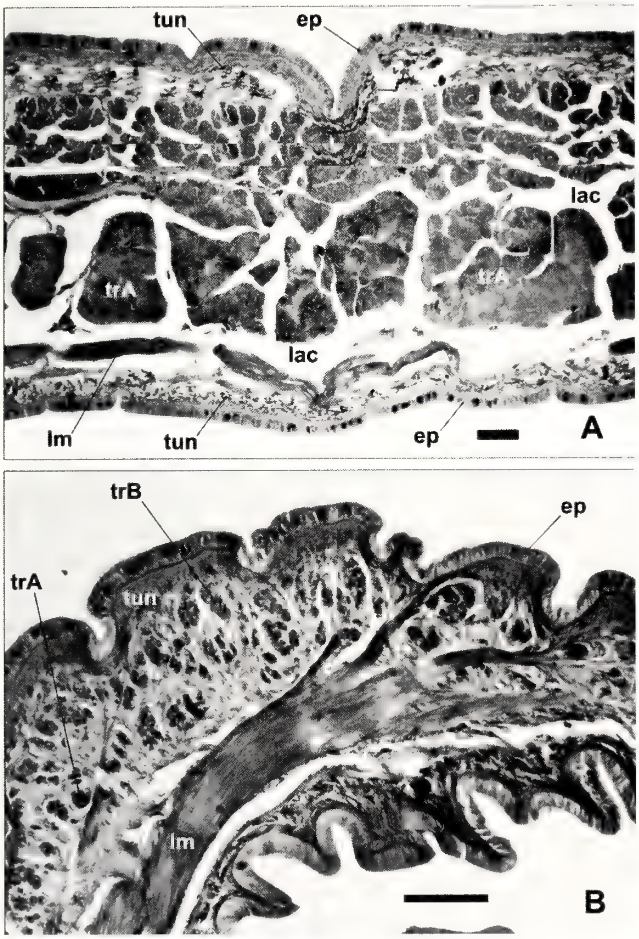

Fig. 7. Micrographs of a frontal section of the wing of *Nautilus pompilius* (the outer side of the wing is on the bottom and the inner side is on the left). A. Middle part of the wing; scale bar = 100 µm. B. Distal margin of the wing. Abbreviations: ep, epithelium; lac, hemolymph lacunae network; lm, longitudinal muscle; trA, transverse muscle of type A; trB, transverse muscle of type B; tun, tunic.

lacunae (Fig. 7). Both sides of the wing are covered by simple epithelium and an underlying thick collagen tunic. The structure of the wing is markedly different in its middle and distal parts. In the middle part the wing is composed of loosely arranged bundles of transverse muscle grouped into two layers, which are approximately equal in thickness. As in the cephalopodium retractors (see histology of the cephalopodium retractors), the muscles in these layers stained differently with Azan; the outer layer stained in reddish-purple and apparently consisted mainly of second type fibers, whereas the inner layer stained in bluish-purple, indicating predomination of the first fiber type (Fig. 7A). The muscular bundles in the outer layer were smaller and penetrated by numerous narrow hemolymph lacunae, whereas the bundles in the inner layer were larger and surrounded by spacious lacunae. On the inner side of the wing, between the layer of transverse bundles and the tunic, there is a narrow layer of longitudinal muscle extending from the proximal part of the wing toward its distal margin (Fig. 7A, B). The surface of the wing in its middle part is rather smooth, but it becomes markedly wrinkled toward the distal margin.

The distal margin of the wing is less muscular than its middle part. It consists mainly of connective tissue with scattered small bundles of transverse muscle of both types (Fig. 7B). The layer of longitudinal muscle becomes fan-shaped, spreading the bundles of fibers toward the outer surface of the wing where they attach to the tunic. Hemolymph lacunae become smaller, accounting for less of the section area than in the middle part. Compared with the cephalopodium retractors and the funnel, the musculature of the wings is simpler, consisting principally of two layers of transverse muscle and one layer of longitudinal muscle. Another peculiarity of the wings is the highly developed system of hemolymph lacunae, completely incorporated into the muscular layers.

Histology of the nuchal retractor

The dorsal and outer lateral surfaces of the nuchal retractors are wrapped by a thick collagen tunic that is in turn covered by a simple columnar epithelium (Fig. 8A). On the inner lateral side of the retractor, the epithelial cells become scale-shaped, covering one another like tiles (Fig. 8B). The core of the nuchal retractor consists of loosely arranged bundles of longitudinal muscles divided by and linked to a network of fibrous connective tissue with hemolymph lacunae. On the inner lateral side of the retractor there is a layer of oblique muscle indistinctly separated from the mass of longitudinal muscle. The muscles account for less than 50% of the cross-section area in the dorsal part of the retractor (Fig. 8A), gradually increasing up to 90% in its ventral part (Fig. 8C). The ventral concave side of the nuchal retractor is covered by an unusual thick non-cellular substance looking comb-like in cross-section and staining intensively blue-violet with Azan. This layer consists of regularly spaced cartilaginous longitudinal wrinkles looking like trabeculae in the cross-sections. The height of the wrinkles ranges from 25 to 30 µm; the width from 4 to 7 µm. The comb-like layer is attached to and apparently produced by vacuolated connective tissue that covers the ventral margin of the retractor muscle.

In summary, the musculature of the nuchal retractors is composed of longitudinal muscle and a small amount of oblique muscle. The radial and transverse muscles are absent. The function of the connective tissue is somewhat remarkable; it forms the matrix embedding the muscles and also secretes a cartilaginous comb-like wrinkled layer on the ventral side of nuchal retractors.

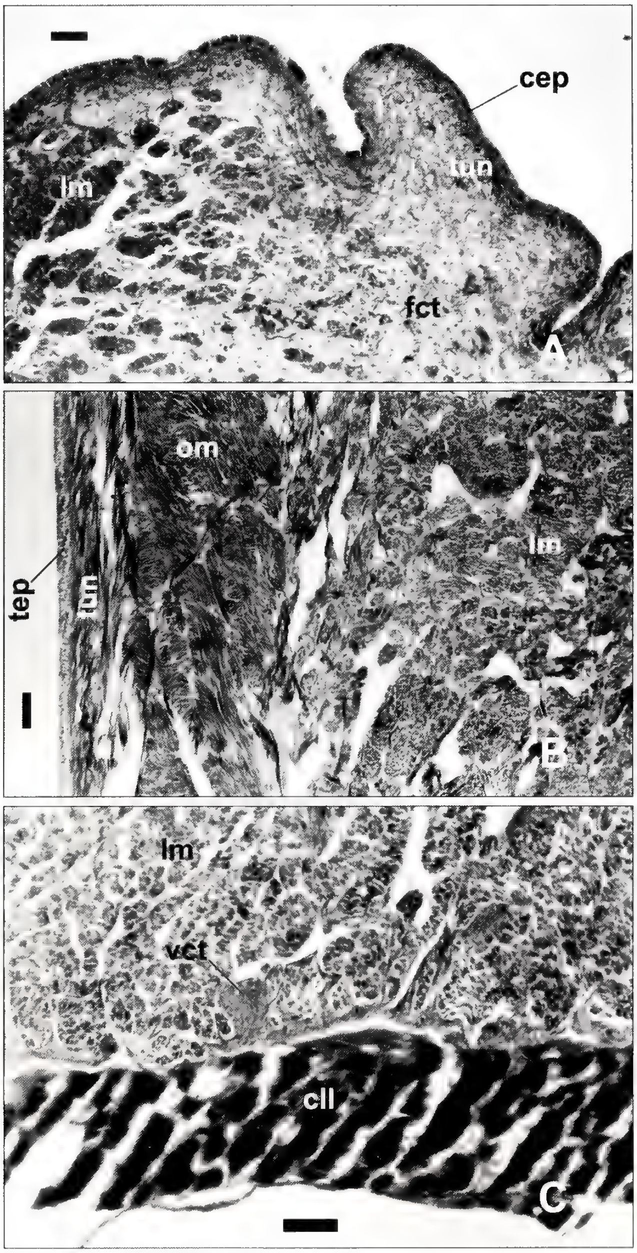

Fig. 8. Micrographs of a transverse section of the left nuchal retractor of *Nautilus pompilius* (all sections are oriented with the outer side of the retractor on the right and ventral side on the bottom). A. Dorsal margin of the nuchal retractor; scale bar = 100 μm. B. Inner margin of the nuchal retractor adjacent to the shell; scale bar = 100 μm. C. Ventral margin of the nuchal retractor; scale bar = 100 μm. Abbreviations: cep, columnar epithelium; cll, comb-like layer; fct, fibrous connective tissue; lm, longitudinal muscle; om, oblique muscle; tep, tile-like epithelium; tun, tunic; vct, vacuolated connective tissue.

DISCUSSION

Comparison of musculature morphology and microanatomy in *Nautilus* with published experimental data on its ventilation and swimming behavior helps us to understand how different components of respiration and locomotion systems may act in different modes of activity.

The cephalopodium retractors are used mainly during jet swimming. Their main function is to perform back-and-forth piston-like movement of the head, generating powerful jet thrust for a short period of time. Another role of the cephalopodium retractors is structural, they form muscular ventro-lateral walls of the visceral sac. Longitudinal and radial muscles act as antagonists. Activation of the longitudinal muscles results in contraction of the retractor muscles, providing a power strike, whereas activation of the radial muscles causes elongation of the retractor muscles. Branching of radial trabeculae, as they approach the outer surface of the retractor, probably serves to distribute the load produced by the radial muscles uniformly over a greater area. Similar arrangements of longitudinal muscle and branching radial trabeculae were found in the digital tentacles of *Nautilus* (Kier, 1988; Fukuda, 1988). The weak development of the radial muscles compared with the longitudinal muscles apparently indicates that elongation of the retractors is, at least partly, due to the elasticity of the soft body. Elastic re-expansion is common in cephalopods and a similar mechanism was proposed as a partial explanation for re-expansion of the squid mantle (Ward, 1972). The absence of oblique muscles reflects an absence of bending or torsion during head retraction. Such movements are impossible indeed, as the concave dorsal side of the hood allows only back-and-forth sliding of the head along the preceding whorl of the shell. The inner and outer layers of transverse muscles probably play a structural role. Tied together by radial trabeculae, they form a muscular framework that holds and shapes the bundles of the longitudinal muscle, insuring the fixed ribbon-like shape of the cephalopodium retractor.

Ultrastructural and metabolic studies of *Nautilus* musculature revealed two distinct types of fibers that can be distinguished by mitochondrial abundance (Hochachka *et al.*, 1978). Type A fibers contain few mitochondria and utilize anaerobic glycolysis for short bursts of jetting, whereas type B fibers contain a large number of mitochondria and utilize aerobic oxidative pathways for sustained submaximal work (Baldwin, 1988). According to Baldwin (1988), 90% of the muscle fibers in the cephalopodium retractor belong to type A. My own data also showed the presence of two morphological types of fibers in the cephalopodium retractor, one type markedly predominating over the other (Fig. 5). Comparing these data with those reported by Baldwin (1988), suggests that the fibers of the first morphological type correspond to type A whereas the fibers of the second type correspond to type B. The presence of different types of muscle fibers in the cephalopodium retractors may be explained functionally and the superficial location of "aerobic" fibers may allow them to be at least partly self-oxygenating. Such a surface respiration is now widely discussed in cephalopods (O'Dor and Hoar, 2000). On the other hand, the superficial position of "aerobic" fibers is beneficial mechanically as it provides them with greater leverage during fiber contraction.

The funnel is used during both respiration and jetting. It is known to be capable of various kinds of movements including expansion and contraction, and undulation and bending (Wells, 1988). In jetting mode, the funnel is pumping water by decreasing its internal volume by rolling itself up like a sheet of paper. The funnel is exposed to substantial loads and has to be safely anchored in the soft body by the funnel cartilage and the funnel retractors. The anatomy of the funnel corresponds to its function. The two most developed muscles, the outer and inner oblique muscles, apparently may act either simultaneously or separately. Since they are composed of crossed bundles with different orientations, their contraction would not result in torsional movement of the funnel. Their simultaneous activation would cause general contraction and rolling up of the funnel itself. Separate activation of the inner or outer oblique muscles would cause inward or outward bending of the funnel fold, respectively. Activation of radial trabeculae may control the thickness of the funnel folds. The bundles of longitudinal muscles are probably responsible for bending of the funnel in any direction. The waving undulation of the funnel folds requires the coordinated activity of transverse, longitudinal, and oblique muscles. During relaxation of the muscles, the thick intermediate layer of connective tissue ensures elastic recoil of the funnel to its resting shape. It also provides the funnel with mechanical strength and elasticity; the latter is especially important for smooth undulating movement.

Baldwin (1988) reported that in the funnel muscle type A and type B fibers occur in equal numbers. However, my study did not reveal any histological or morphological difference between funnel muscle fibers. In contrast, I found two distinct types of muscle fibers in the wings, each type including about 50% of the fibers (Fig. 7). Baldwin's (1988) data on the distribution of different metabolic types of muscle may correspond to the collar folds and wings rather than to the funnel itself.

The musculature arrangement in the wings is amazingly simple, considering the great variety of undulating and waving movements these structures can perform. Presumably, the widely separated transverse muscle bundles contract independently from one another, and coordinated contraction of different bundles could produce undulating waves running along the wing. The inner layer of longitudinal muscle may allow inward bending of the wing, whereas its distal fan-like part may provide the necessary mobility to the wing margin.

The main function of the nuchal retractors is probably to attach the wings, and particularly the nuchal valves to the shell, monitoring their positions and preventing them from turning inside out during jetting. The only possible movement for the nuchal retractors is longitudinal contraction-extension. Any bending or torsion is disallowed by the very position of these muscles in the animal body. Contraction is achieved by the longitudinal muscles that compose the bulk of the nuchal retractors (Fig. 8). Absence of muscle antagonists suggests that their re-expansion occurs passively, through elastic recoil of deformed connective tissue. The dorsal mantle cavity forms two narrow tubes around the nuchal retractors that apparently allow them to move independently from the surrounding tissue (Fig. 4A, B). The unusual scale-like epithelium on the inner side of nuchal retractors (Fig. 8B), and the non-cellular comb-like layer on the ventral side of nuchal retractors may serve to minimize friction. In fresh animals the tubes are filled with a mucous substance that probably serves as lubricant.

The gills in *Nautilus* are adapted to work at low velocities of ventilatory flow. The gills make an almost complete barrier between prebranchial and postbranchial chambers, creating considerable drag forces as water passes through, and, unlike the gills in coleoid cephalopods, are not fixed firmly in their position. The pressures generated by ventilatory flows are quite low, less than 0.1 kPa (Packard *et al.*, 1980; Wells and Wells, 1985). Nevertheless, observations showed that even these pressures caused the gills to move downward when the water is expelled from the collar pockets (Wells, 1988).

The mantle cavity functions in different ways during respiration and jetting. During ventilation, the gills divide the mantle cavity into the prebranchial and postbranchial chambers. As the same volume of water consequently passes from prebranchial into the postbranchial chambers, the total volume of the mantle cavity does not change considerably and the volume of a single stroke is small. During jetting, the peak pressures are one or two orders of magnitude higher than in quiet ventilation (Packard *et al.*, 1980; Chamberlain, 1988). Wells (1988) suggested that under such pressures the gills may be displaced from their normal position. As one may see from the total cross-sections of *Nautilus* (Fig. 3B), the strong flows from the collar pockets would force the gills against the ventral mantle wall and consequently allow the water to pass relatively unimpeded directly to the funnel. As a result, the mantle cavity would function as a single volume, expanding and contracting following the piston-like movement of the cephalopodium. The mantle does not take part in contraction. It just seals itself to the inner shell surface, minimizing water pressure loss during jetting. Displacement of the gills during jet-swimming has important functional consequences since the oxygen extraction rate falls to 4-7%, whereas at quiet respiration it constitutes 9-12% (Wells, 1988). This decline of oxygen extraction is the most likely reason why *Nautilus* cannot maintain jet-swimming for more than a few minutes.

Wells (1988) reported that when *Nautilus* rests after a period of activity its oxygen extraction rate reaches the highest level, 20% or more. During this time the head moves in and out of the mantle cavity, the hood rising and falling rhythmically in time with the ventilation cycle. This breathing pattern differs from quiet respiration both in soft body action and in oxygen extraction efficiency. Movement of the head and the hood indicates action of the cephalopodium retractors, as in jetting, yet a high oxygen extraction rate indicates that the gills are not displaced from their working position. My observations on live *Nautilus pompilius* in the Hakkeijima Public Aquarium (Tokyo) resolved this apparent contradiction. If the animal is breathing deeply after a period of jetting, its funnel aperture always remains wide open. On the contrary, if the animal is jetting, the funnel aperture increases only slightly at the beginning of a jet pulse, and then contracts again during the water expulsion. The wide opening of the funnel reduces the pressure in the mantle cavity (Chamberlain, 1988), and minimizes the propulsive thrust with resulting flows that are gentle and do not displace the gills from their normal position. After several minutes of deep breathing *Nautilus* gradually changes to quiet respiration until the next period of activity.

The inability of the gills to work at high pressures and flow velocities makes them a weak point in both the respiration and locomotion systems of *Nautilus*, with implied constraints on its organization. The flexible support of the gills made intensification of the ventilatory flows impossible, but also restricted the jet propulsion as the primary means of locomotion. Apparently, the evolutionary answer of *Nautilus* to the dilemma "to breathe or to move" was the development of a special ventilation pattern and life style that combined breathing with slow sustained swimming. Powerful jetting by means of the cephalopodium retractors remained as an accessory system used for short bursts of rapid swimming, usually associated with danger. Respiration and locomotion systems of *Nautilus* exhibit a set of archaic morphological and functional features. *Nautilus* jets using the cephalopodium retractors that are homologous with the columellar shell muscles of gastropods and monoplacophorans. The jet thrusts are generated by piston-like movements of its head into the mantle cavity, a rather primitive and uneasy mode of locomotion. Coleoids acquired muscular mantles that function for jet swimming and generation of ventilatory flows. The cephalopodium retractors in coleoids have lost the jetting function and are reduced to thin, membranous muscular integument enclosing the digestive gland (Bizikov, 1996). Remarkably, in some squid families (Onychoteuthidae, Ommastrephidae, Gonatidae, Cranchiidae) the cephalopodium retractors are still functional at young stages, allowing squids to pull their heads deep inside the mantle cavity (Nesis, 1987; Arkhipkin and Bizikov, 1996). The structure of the funnel and the gills of *Nautilus* show a transitional stage between typically molluscan and cephalopod organization.

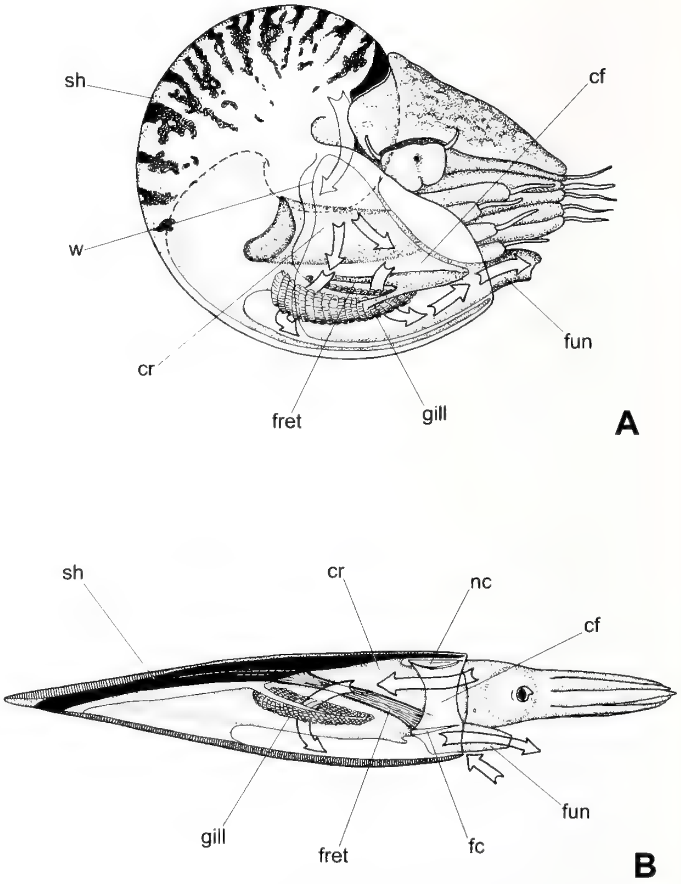

Fig. 9. The swimming and breathing mechanism of cephalopods. The arrows show the water flows during breathing and swimming. A. *Nautilus*, modified from Wells (1988). B. Squid, modified from Naef (1923). Abbreviations: cf, collar fold; cr, cephalopodium retractor; fc, funnel cartilage; fret, funnel retractor muscle; fun, funnel; gill, gill; nc, nuchal cartilage; sh, shell; w, wing.

The ventilation flow pattern in *Nautilus* is similar to that found in coleoids (Fig. 9); the water enters the mantle cavity through the slits between the collar folds and the mantle, passes to the ventral part of the mantle cavity, flushing the gills, and is then expelled through the funnel. The collar folds in *Nautilus* function both generating the flows and as valves, whereas in most coleoids they act mainly as valves, opening and closing the slits on the lateral sides of the head. The gills in both groups are situated in a similar position, ventral to the funnel retractors. However, in coleoids each gill is attached to the mantle along its entire length. Such an alignment allows the gills to withstand high flow velocities and pressures, and function in all modes of animal activity. The funnel in *Nautilus* is not a real tube, as in coleoids, but a triangular muscular fold that is rolled into a tube. In *Nautilus* the funnel performs two functions, generating the respiratory flows and monitoring the jetting, whereas in coleoids it is used mainly for jetting control. The funnel retractors in *Nautilus* are rather weak, attaching to the ventral surface of the cephalopodium retractors. On the contrary, in coleoids they are well developed and attach directly to the gladius (or sepion), safely fixing the funnel in its position during jetting. There is an obvious topographic similarity in the position of the three pairs of retractors between *Nautilus* and coleoid cephalopods. In both groups the funnel retractors pass along the lateral surface of the cephalopodium retractors and fuse with them near the shell (Bizikov, 1996). The nuchal retractors occupy similar positions in *Nautilus* and coleoids. In squids they attach to the inner side of the median plate of the gladius, adjusting the position of the nuchal cartilage during respiration and jetting (Bizikov and Arkhipkin, 1997). Thus, *Nautilus* and coleoid cephalopods exhibit similar morphological Bauplans, but differ essentially in functional design of locomotion and respiration systems.

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Effects of temperature on duration of viability for glochidia of freshwater mussels (Bivalvia: Unionidae)

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Abstract: Glochidia from gravid females of *Villosa iris* (Lea, 1829) and *Actinonaias pectorosa* (Conrad, 1834) were extracted from marsupia and tested for viability over several days. Glochidia that were flushed from the gill and those retained in the excised gill marsupium were tested at three holding temperatures: 0°, 10°, and 25°C. Viability was tested by exposing glochidia to a sodium chloride solution, and then confirmed by infesting known host fish with glochidia at 1 week and 2 weeks post-extraction from the female mussel. Results indicate that extracted glochidia remained viable for significantly longer than excised intra-marsupial glochidia. There was no significant difference in viability of glochidia between 0° and 10°C in extracted treatments ($p > 0.05$). Extracted glochidia of *V. iris* maintained >75% viability for 180, 192, and 46 hr at 0°, 10°, and 25°C, respectively. Similarly, glochidia extracted from *A. pectorosa* maintained >75% viability for 345, 310, and 108 hr at 0°, 10°, and 25°C, respectively. Long-term viability of glochidia would promote downstream dispersal and has practical applications in captive propagation.

Key Words: Unionidae, freshwater mussels, *Villosa, Actinonaias*, glochidia viability

Freshwater mussels have a complex reproductive cycle involving an obligate parasitic larval stage. The cycle begins by the release of sperm by males into the water column, which are subsequently siphoned by females of the same species to fertilize the eggs. Fertilized eggs are then brooded in the gill marsupium until they reach the larval stage (glochidium). Fully developed glochidia are released for intended attachment to the gills or fins of a suitable host fish. The duration of encystment is dependent on species and water temperatures. After 2-6 weeks of encystment, the glochidia transform to juvenile mussels and drop to the substratum to begin the free-living juvenile stage.

The viability of glochidia after release and prior to attachment has been reported only as anecdotal comments (Murphy, 1942; Matteson, 1948; Tedla and Fernando, 1969). Although these studies indicate that longevity of extracted glochidia may exceed 1 week, the methods and percent viability are inadequately defined and inconclusive. The purpose of this study is to determine longevity of glochidia at three water temperatures, conducted with glochidia retained within the excised gill and glochidia extracted from the gill marsupium.

METHODS

The viability of glochidia over time was tested at three water temperatures and for two modes of exposure. Temperature treatments were conducted in a low temperature incubator (Fisher Scientific Model 307) at 25°C, a refrigerator at 10°C, and a cooler filled with ice at near 0°C. Modes of exposure included an extracted treatment, referring to glochidia that were flushed from the gill marsupium; and an intra-marsupial treatment, in which the entire marsupial gill was excised and samples of glochidia were extracted at designated intervals. These trials were conducted twice; first using the rainbow mussel, *Villosa iris* (Lea, 1829), and then with the pheasantshell, *Actinonaias pectorosa* (Conrad, 1834). Both species are long-term brooders (bradytictic), with fully developed glochidia in gravid females from fall through spring (Parmalee and Bogan, 1998).

Eighteen gravid specimens of *Villosa iris* from Indian Creek, Tazewell County, Virginia, were collected in April 1999 and held in a Living Stream (Frigid Units, Toledo, OH) at 13°C at the Virginia Tech Aquaculture Center. The Living Stream contained a 50:50 mixture of well water and dechlorinated town water (Blacksburg, Virginia) to achieve a hardness of approximately 250 mg/l. This mixed water was used in all experiments. Mussels were held for 24 h and then transported to the laboratory for testing. In the laboratory, each gravid mussel was opened by cutting posterior and anterior adductor mussels; 1 gill was excised intact and placed in a petri dish with 5 cm of water from the Living Stream (13°C). This was adequate water to immerse the gill, and to allow subsamples of glochidia to be extracted. The second gill was punctured with a large bore (20 gauge) needle and syringe, and glochidia were gently flushed with water into a petri dish. A subsample of glochidia from each dish was tested to confirm viability using a saturated solution of sodium chloride (Lefevre and Curtis, 1910; Zale and Neves, 1982). Live glochidia, normally in an open (gaping) position, will clamp shut when exposed to saline solution. Once viability was determined, dishes containing glochidia were randomly assigned to a temperature treatment (0°, 10°, and 25°C). Six replicate dishes were used for each of the three temperature treatments and for both extracted and intra-marsupial glochidia treatments, for a total of 36 dishes.

A second trial was conducted in January 2000, using *Actinonaias pectorosa* collected from the Middle Fork Holston River, Washington County, Virginia. This second trial was conducted in an identical fashion to the first, except that only extracted glochidia were tested. Eighteen gravid *A. pectorosa* were collected, and held in the Living Stream at 13°C prior to glochidial extraction. Since the intra-marsupial treatment was not replicated, sacrifice of the animal was not necessary. Glochidia were extracted by gently prying apart the valves, inserting the large bore needle into the water tube of one of the gills, and flushing it with water. Glochidia were collected in a petri dish, tested for viability (as described above), and randomly assigned to a temperature treatment. Six replicates of each temperature treatment were tested, for a total of 18 dishes.

Samples of glochidia from both species were tested for viability at 0, 0.5, 1, 3, 6, 12, 18, 24 h and at 6 h intervals thereafter, until 96 h post-extraction. To ensure an adequate number of glochidia for the duration of the experiment, the sampling interval was increased from 6 h to 12 h after 96 h. Observations continued for 320 h and 474 h for *Villosa iris* and *Actinonaias pectorosa*, respectively. At each observation interval, a subsample of approximately 75 to 100 glochidia was removed from each of the extracted glochidia treatments using a Pasteur pipette and then placed on a clean petri dish. Glochidia from the intra-marsupial treatment were extracted by inserting a large bore needle into the water tube and gently sucking out a small sample at each observation interval. Glochidia from all water tubes were assumed to be mature. From the subsample, an initial count of 25 glochidia was made, noting any closed individuals. A saturated solution of sodium chloride then was added, and after 10 s, the 25 glochidia were recounted to records the number of open and closed individuals. Individuals remaining open after the addition of sodium chloride were considered to be functionally dead, as were individuals closed before the addition of sodium chloride. These individuals may not have been dead; however, a closed or unresponsive glochidium is incapable of attaching to host fish (Jacobson *et al.*, 1997).

To confirm the viability of glochidia after 1 week and 2 weeks post-extraction, a sample of glochidia from two randomly selected replicates of both the 10° and 0°C extracted treatments was used to infest known host fish and to confirm attachment to gills and metamorphosis. Glochidia from the 25°C trial and the within-gill treatment were not tested, as they were all dead at 1 week of testing. For the *Villosa iris* infestations, 8 rock bass *(Ambloplites rupestris)* collected from the New River (Pulaski County, Virginia) were infested. For *Actinonaias pectorosa*, 24 banded sculpin *(Cottus carolinae)* from the North Fork Roanoke River (Montgomery County, Virginia) were used. All fish were collected using a backpack electroshocker (Smith Root model 15-D). Zale and Neves (1982) identified rock bass to be a successful host for *V. iris*, and banded sculpin were confirmed as a host for *A. pectorosa* by J. Layzer (pers. comm., Tennessee Tech). Glochidia were pipetted directly onto the gills of the fish. Two fish were infested with glochidia from each of the treatments used, and fish from each treatment were held in separate 38 l tanks. The gills of the infested fish were examined on days 1, 2, and 3 post-infestation to ensure encystment of glochidia. Average water temperature in the tanks for the *V. iris* infestations was 24°C; temperature was maintained at 21°C for *A. pectorosa*. Once encystment was confirmed, the bottom of each tank was siphoned beginning eight days post-infestation, and the siphonate was passed through a 105 µm sieve to collect newly metamorphosed juveniles or sloughed glochidia.

Survival of glochidia was non-normal, non-continuous, and binary (alive vs. dead); therefore, data were modeled by logistic regression analysis (PROC GENMOD; SAS Institute, 1988). No correlation was necessary, as new glochidia were used at each sampling interval. Goodness of fit was evaluated using a deviance test (SAS Institute, 1988). Pair-wise differences between treatments were assessed using scaled Wald tests. The scale parameter increases the calculated Z statistic, thereby making probability estimates more conservative to compensate for any potential lack of fit to the model (DSCALE option, PROC GENMOD). The level of significance for all statistical tests was set at $\alpha = 0.05$.

RESULTS

Survival of *Villosa iris* glochidia differed significantly between extracted and intra-marsupial treatments (Table 1). For both species, significant differences occurred between the 25°C and the 0°C treatments, and also between the 25°C and 10°C treatments (Table 1). However, there was no significant difference between the survival of extracted glochidia held at 0° and 10°C for either species.

Table 1. Number of hours that viability of glochidia remained above 75%. Times within a row followed by different letters were significantly different ($p < 0.05$; Wald Z test).

	Holding temperature (°C)		
Trials with glochidia	0°	10°	25°
Villosa iris (within gill)	41^{a}	98^{b}	28^{c}
V. iris (extracted)	180^{a}	192^{a}	46^{b}
Actinonaias pectorosa (extracted)	345^{a}	310^{a}	108^{b}

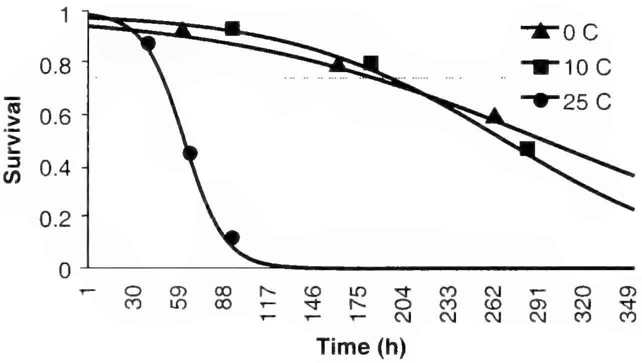

Fig. 1. Model-generated survivorship curves for the extracted glochidia of *Villosa iris*. Dashed line indicates 75% viability.

The viabilities of glochidia over time for *Villosa iris* and *Actinonaias pectorosa* were similar and consistent. In all cases, the 0° and 10°C treatments had similar trends, and greatly outlived glochidia in the 25°C treatments (Table 1). For comparison of treatments and species, we selected 75% viability as a lower threshold. The 75% viable cutoff is a somewhat arbitrary value; however, we consider it to be a practical threshold when using glochidia for infestations, where further mortality of glochidia would negate any benefits of *in situ* extractions. Extracted glochidia of *V. iris* maintained >75% viability for 180, 192, and 46 hr at 0°, 10°, and 25°C, respectively (Fig. 1). The intra-marsupial treatment maintained >75% viability for a shorter period; namely, 41, 98, and 28 hr at 0°, 10°, and 25°C, respectively (Fig. 2). After approximately 24 h, gill tissue and glochidia of the intra-marsupial treatments exhibited extensive bacterial growth and tissue decay. This decay and the reduced period of glochidial viability compelled us to omit the intra-marsupial treatment during our *A. pectorosa* trials. Viability of extracted glochidia for *A. pectorosa* remained >75% for 345 hr at 0°C, 310 hr at 10°C, and 108 hr at 25°C (Fig. 3).

Verification of the viability of glochidia was confirmed through subsequent host fish infestations. Glochidia transformed to juveniles in all *Villosa iris* treatments, from 13 days to 18 days post-infestation, and for *Actinonaias pectorosa* from 16 days to 23 days post-infestation.

DISCUSSION

Our experiments demonstrate that the duration of viability of glochidia is considerably longer than documented in previous studies (Table 2). Results of these studies indicate that there is some variability in longevity among species, but all tested species maintain some level of viability for at least one week when held at cool temperatures. Tedla and Fernando (1969) tested glochidia of *Lampsilis radiata siliquoidea* (Barnes, 1823) and reported that few were able to infest host fish after 9 days at 10°C; none survived more than 24 h at 25°C. Murphy (1942) tested *Margaritifera falcata* (Gould, 1850) held at 11.2°C, and reported that some glochidia remained viable after 11 days. Matteson (1948) reported that extracted glochidia of *Elliptio complanata* (Lightfoot, 1786) remained alive after seven days when held at 4.5°C. Although these studies were not designed specifically to address life span of glochidia, they seem to indicate considerable variation among species. Differences in longevity and viability of glochidia in these studies emphasize the likely variability among species and its correlation with water temperatures. The longevity of viable glochidia differed greatly between the 2 species and 3 temperatures tested in our study. Extracted *Actinonaias pectorosa* glochidia remained viable almost twice as long as extracted glochidia of *Villosa iris* at the same temperatures, and both species showed significant differences in viability over time between the 0° and 10°C treatments and the 25°C treatment. Both species used in this

Table 2. Comparison of longevity of glochidia between previous studies and this study.

Mussel Species	Duration of viability (days)	Temperature (°C)	Viability (%)	Citation
Margaritifera falcata	11	11.2	not reported	Murphy (1942)
Elliptio complanata	7	4.5	not reported	Matteson (1948)
Lampsilis r. siliquoidea	9	10	1.2	Tedla and Fernando (1969)
Villosa iris	7.5	0	75	This study
	8	10		
Actinonaias pectorosa	14.4	0	75	This study
	12.9		10	

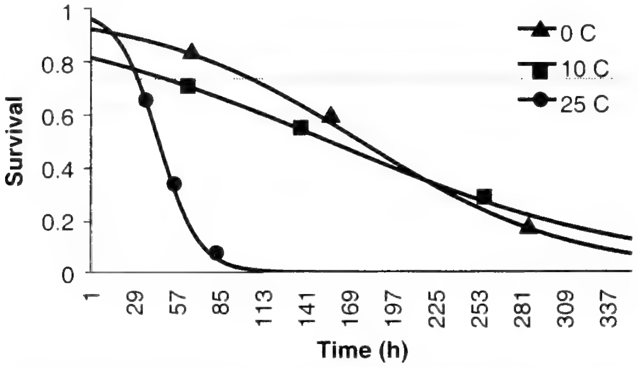

Fig. 2. Model-generated survivorship curves for the glochidia of *Villosa iris* retained within the gill. Dashed line indicates 75% viability.

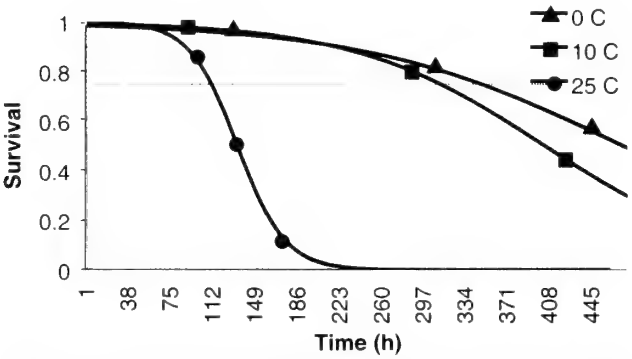

Fig. 3. Model-generated survivorship curves for the extracted glochidia of *Actinonaias pectorosa*. Dashed line indicates 75% viability.

study are bradytictic, with glochidia overwintering in the gills of a female mussel for up to six months. It is possible that tachytictic species (summer brooders) may have a shorter duration of viability.

The long-term viability of extracted glochidia has obvious implications for captive propagation. Production of juvenile mussels typically involves the collection of gravid females from the wild, and then transport to the laboratory where glochidia are extracted and used to infest host fishes. In light of our findings, it is not essential that gravid female mussels be transported from the collection site, as glochidia can be flushed from the gills by hypodermic syringe at streamside, returning only the extracted glochidia to the laboratory. This is particularly applicable to federally listed species, where handling stress, distance of travel, and other factors may jeopardize the health and survival of individuals (Chen *et al.*, 2001). If glochidia are extracted and transported in cooled water (0-10°C), they can remain viable for infestation for several days without reduction in attachment success. Removing glochidia on site eliminates transport stress to the gravid mussel and the need for a return trip to release specimens. It should be possible also to chill and ship extracted glochidia to a propagation facility, such that infestations can occur at a distant laboratory or propagation facility. The time that glochidia remain viable also is useful when a gravid mussel aborts glochidia after removal from the substratum, during transport, or in captivity. As long as the mature glochidia are collected and held at cool temperatures, they can be used over an extended period to infest host fish.

Long-term viability of glochidia also is important from a life history perspective. Previously, longevity of expelled glochidia was thought to be approximately three days, providing limited opportunity for downstream drift, dispersal, and incidental contact with proximate fishes (Neves and Widlak, 1988). However, if glochidia remain viable for up to two weeks in cool water (spring or fall), there is a greater opportunity for dispersal of glochidia between suitable shoals where mussel aggregations and host fish typically occur. Greater distances of dispersal to contact host fishes would thereby extend the range and potential for genetic mixing between localized demes. These greater dispersal distances would be especially important for long-term brooders that release glochidia in spring when flow is high and water temperatures are cool. Further testing of viability of glochidia of other species, particularly tachytictic species, is needed to confirm lengthy periods of viability and the adaptive significance of this life stage to the reproductive success and genetic integrity of mussel populations.

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The endangered partulid tree snail *Samoana thurstoni* (Cooke and Crampton, 1930) on Olosega and the land snail diversity of the Manuʻa Islands, American Samoa*

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Abstract: Survey work on the American Samoan island of Olosega, one of the three Manuʻa Islands (Taʻū, Ofu, Olosega), increased the known land snail fauna of the island from 6 to 30 species. Of these species, 17 are native to the islands and 13 are introduced. Most notable was the discovery of *Samoana thurstoni* (Cooke and Crampton, 1930) (Partulidae), previously considered an Ofu endemic. The entire land snail fauna of Manuʻa is composed of 45 species, with 40 on Taʻū, 32 on Ofu, and 30 on Olosega. The three islands have 23 species in common. Endemism is low. Each island appears to have a random subset of the total species, though this may partly reflect a need for further survey work as well as true randomness in the natural construction of the faunas. While some native species seem to be extinct, others are surviving. However, the faunas of all three islands, especially the ground-level faunas, are dominated by alien species, notably species of Subulinidae. That such a relatively accessible island as Olosega should yield so many new records suggests that additional survey work is necessary throughout much of the Pacific before we can have the baseline inventory of Pacific land snail biodiversity necessary for its conservation.

Key Words: biodiversity, conservation, land snail, Pacific, Partulidae, Samoa, *Samoana*

The Samoan archipelago lies in the south-central Pacific Ocean and is divided politically between Samoa (formerly Western Samoa) and American Samoa. The native land snail fauna of the islands includes numerous endemic species, but a number of widespread alien species are also present (Cowie, 1998, 2001a).

This paper focuses on the Manuʻa group of American Samoa, with three main islands: Ofu, Olosega and Taʻū (Fig. 1). Until recently, the land snail faunas of these islands were poorly known. Although large collections, from Taʻū in particular, had been made in the early 20th century and are held in the Bishop Museum (Honolulu), little had been published on the faunas as a whole. Cowie (1998) listed all species reported from the Samoan archipelago in the literature up to 1997, giving island by island distributions as far as could be ascertained from that literature. Subsequent field work (Cowie and Cook, 1999, 2001; Cowie, 2001a) on Ofu and Taʻū, as well as Tutuila (the main island of American Samoa) and the adjacent small island of Aunuʻu (Cowie and Rundell, 2002), extended this knowledge of the faunas of these islands. This work demonstrated the precarious nature of some of the species, especially the four species of Partulidae, the decline of most native species, and the increase and continued introduction (Cowie, 2001a) of a relatively small number of widespread alien species.

None of this previously reported work has included more than scanty collecting on Olosega, the fauna of which thus remains almost unknown. Only six species have been recorded from Olosega in the literature (Cowie, 1998).

This paper reports on the land snail species collected during field work on Olosega in the early 2001, provides a faunal inventory for island based on these new collections and on earlier collecting, and compares the land snail fauna of Olosega with the faunas of the other Manuʻa Islands.

METHODS

Field survey work was undertaken on Olosega in February and April 2001. Samples of snails were taken at

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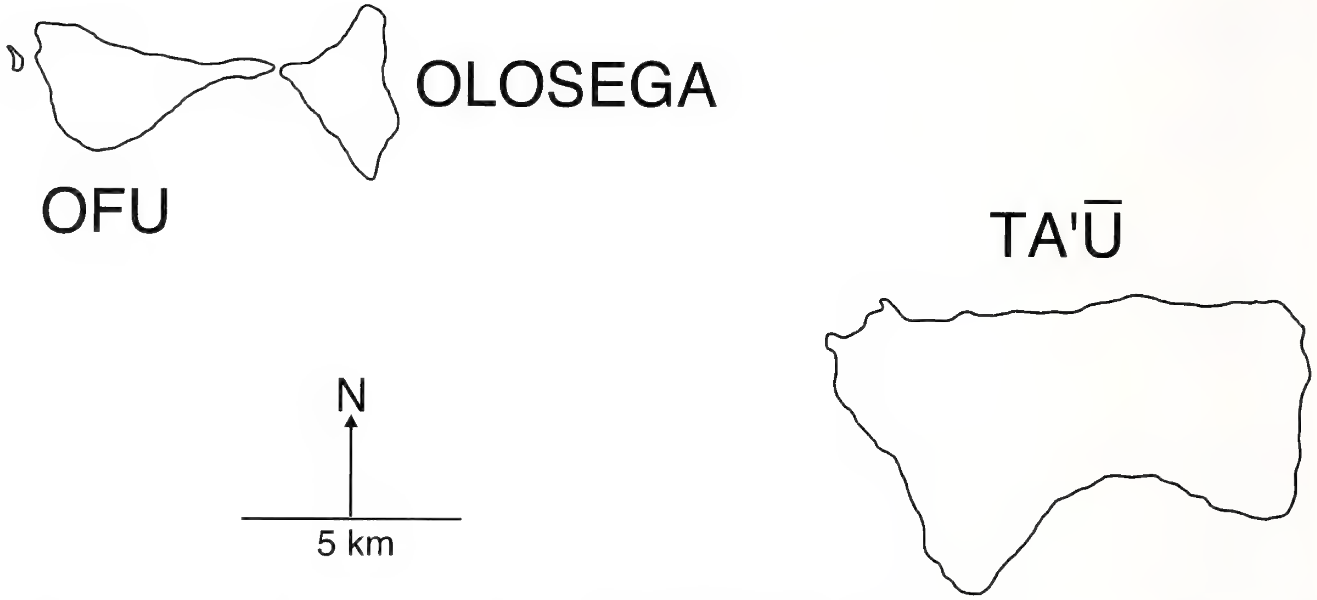

Fig. 1. The Manu'a Islands of American Samoa. The islands lie between 169° and 171° W and between 14° and 15° S. Tutuila, the main island of American Samoa lies approximately 100 km to the west of the Manu'a Islands.

14 locations on the island (Fig. 2). These locations ranged from lowland coastal habitats to the highest point on the island (elevation 634 m).

Collecting protocols followed Cowie and Cook (1999, 2001) and Cowie (2001a), essentially involving timed hand collecting from vegetation and from the ground-level litter and upper soil levels. This study, as those previous studies, was intended as a species inventory survey. Therefore, in the interests of maximizing number of species detected per unit effort, no litter/soil samples were taken for laboratory analysis (cf. Emberton *et al.*, 1996; Cowie, 2001a). At most sampling stations, the field team of 4 to 6 people searched the above-ground vegetation for 10 min and the ground-level litter/soil for an additional 10 min. Untimed samples were taken incidentally when interesting snails/slugs/shells were encountered (including one sample on Ofu). In addition, while moving through the forest, vegetation was continually scanned for tree snails, especially Partulidae.

The samples were returned to the laboratory for sorting and identification, with confirmation of identifications based on comparison with previously identified material (including type material) in the extensive Pacific island land snail collections of the Bishop Museum (Honolulu).

All samples have been deposited in the Bishop Museum mollusc collections (accession number 2001.067; catalog numbers BPBM 261780-261851). Representative specimens of most species were also deposited at the American Samoa Community College (Land Grant Program) and at the National Park of American Samoa.

In addition, previous collections from the Manu'a Islands held at the Bishop Museum were reviewed and the database of the land snail collections of the Field Museum (Chicago), the only other major museum with large holdings of Samoan land snails, was scanned for records.

RESULTS

Species recorded on Olosega

Table 1 lists the species collected on Olosega during the 2001 survey, as well as those previously known from the island. It also indicates their biogeographic status: endemic (occurs naturally only in the Samoan archipelago), indigenous (occurs naturally in the Samoan archipelago but also elsewhere), alien (artificially introduced to the Samoan archipelago), cryptogenic (of unknown native or alien origin - Carlton, 1996).

Prior to this study, only six species of land snails had been reported in the literature from Olosega (Table 1). Of these, three were native, two were cryptogenic (probably introduced by early Polynesian colonizers though they may occur in the Samoan Islands naturally), and one was a more recent, probably late eighteenth or nineteenth century, introduction. Twelve additional unreported species are represented by previous collections in the Bishop Museum (Table 1); of these species seven are native, one is cryptogenic, and four are alien.

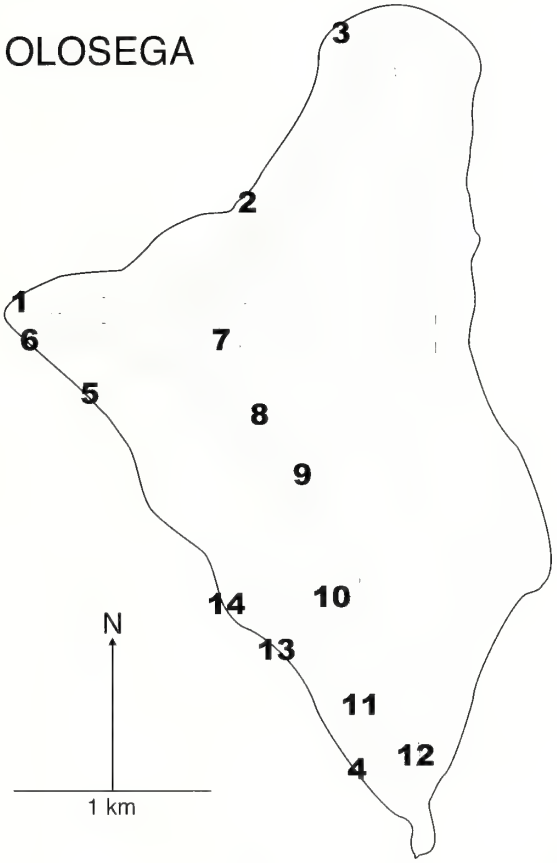

Fig. 2. Numbered sampling stations on Olosega. Contours at 122 m (400 ft) intervals.

The 2001 survey collected 22 species (Table 1), including 3 of the 6 previously recorded in the literature, 7 of the 12 previously collected but unreported, and 12 newly recorded species. Of these newly recorded species, seven are native and five are alien.

The most notable find was *Samoana thurstoni* (Partulidae), found at three mid- to high-elevation sampling stations (stations 8, 9, and 10; c. 300-500 m). At each of the two stations (9, 10) at which live individuals were found during the regular sampling, an additional 30 min of searching was undertaken by 5 members of the field team, but no additional *S. thurstoni* were found. A total of six live individuals was recorded, including three adults, two subadults, and one small juvenile. Four dead shells were also found at station 10 and a single dead shell was found at station 8. The habitat was mid-elevation forest (not cloud forest) with a relatively open understory and an incomplete canopy. Most *S. thurstoni* individuals were associated with the endemic Samoan tree *Syzygium samoense* (Burkhill) Whistler. No partulids were previously known from Olosega (Cowie, 1998), and *Samoana thurstoni* was previously known only from the summit of Ofu, where it is extremely rare and threatened (Cowie and Cook, 1999, 2001).

Notable absences in the 2001 survey were three of the six species previously reported: *Minidonta manuaensis* Solem, 1976 (Endodontidae), *Discocharopa aperta* (Möllendorff, 1888) (Charopidae), and *Lamellidea oblonga* (Pease, 1865) (Achatinellidae). Also, neither the giant African snail, *Achatina fulica* Bowdich, 1822, nor the alien predatory snail *Euglandina rosea* (Férussac, 1821) was recorded.

The study increased the reported land snail fauna of Olosega from 6 to 30 species.

The faunas of Taʻū, Ofu, and Olosega

The entire fauna of Manuʻa includes 45 land snail (and slug) species (Table 1). Taʻū has 40 species, Ofu 32, and Olosega 30. Of these species, 23 are found on all 3 islands and 34 on at least 2 islands.

Endemism is low: only three species are endemic to Manuʻa (*Samoana thurstoni, Minidonta manuaensis, Sinployea clausa* Solem, 1983), with two additional possible endemics (*Pleuropoma* n. sp., *Omphalotropis* sp.), and one subspecific endemic (*Sinployea allecta tauensis* Solem, 1983). Only *Sinployea clausa* is endemic to a single island, although *Pleuropoma* n. sp. may be, and *Sinployea allecta tauensis* is a single-island endemic at the subspecific level.

Of the seven species recorded from Taʻū only, three are or may be endemic to the island (*Pleuropoma* n. sp., *Sinployea clausa, S. allecta tauensis*, see above). The other four are widespread species, either alien (*Achatina fulica, Euglandina rosea*) or native [*Allochroa layardi* Adams and Adams, 1855, *Coneuplecta microconus* [Mousson, 1865]). Three species are recorded from Ofu only: *Tralia costata* (Quoy and Gaimard, 1832) is a naturally widespread Pacific species; *Eua zebrina* (Gould, 1847) is known also from Tutuila; and *Bradybaena similaris* (Rang, 1831) is a widespread alien in the Pacific. Only one species, *Ovachlamys fulgens* (Gude, 1900), is recorded from Olosega only; it is an increasingly widespread alien in the Pacific and elsewhere, including Tutuila.

A large proportion of the fauna is alien. Of the 45 species recorded from Manuʻa, only 26 are native. The other 19 include 13 alien species and 6 cryptogenic species. Proportions of native to alien/cryptogenic species are not significantly different (log-likelihood G test) on the 3 islands: Taʻū – 24:16, Ofu – 18:14, Olosega – 16:14.

DISCUSSION

This study of Olosega and the recent surveys of Taʻū and Ofu (Cowie and Cook, 1999, 2001; Cowie, 2001a) constitute the most comprehensive land snail survey of

Table 1. Species of land snails from Taʻū, Ofu, and Olosega, with biogeographic status in the Samoan archipelago (see text for explanation of terms). Abbreviations: S, data from the 2001 survey; R, previous records in the literature (Cowie, 1998, 2001a); B, additional previously unpublished records from the malacological collections of Bishop Museum; F, unpublished information from the on-line database of the malacological collections of the Field Museum, Chicago.

Family/species	Taʻū	Ofu	Olosega	Status
HELICINIDAE				
Orobophana musiva (Gould, 1847)	R	R	B, S	endemic
Pleuropoma beryllina (Gould, 1847)	R		S	indigenous
Pleuropoma fulgora (Gould, 1847)	R	R	R, S	indigenous
Pleuropoma n. sp.	R			endemic/indigenous
TRUNCATELLIDAE				
Truncatella guerinii Villa and Villa, 1841	R	R	S	indigenous
ASSIMINEIDAE				
Assiminea parvula (Mousson, 1865)	R	R	B	indigenous
Omphalotropis sp.	R	R	B	endemic/indigenous
VERONICELLIDAE				
Vaginulus plebeius Fischer, 1868[a]	R	S	S	alien
ELLOBIIDAE				
Allochroa layardi Adams and Adams, 1855	B			indigenous
Laemodonta monilifera (Adams and Adams, 1854)[b]	B	B		indigenous
Melampus castaneus (Megerle, 1816)	R	R		indigenous
Melampus fasciatus (Deshayes, 1830)	R	R	S	indigenous
Melampus luteus (Quoy and Gaimard, 1832)	B	B	S	indigenous
Pedipes sandwicensis Pease, 1860	B	B		indigenous
Pythia scarabaeus (Linnaeus, 1758)	R	R	S	indigenous
Tralia costata (Quoy and Gaimard, 1832)		R		indigenous
ACHATINELLIDAE				
Elasmias sp.	R	R		cryptogenic
Lamellidea oblonga (Pease, 1865)	R		R	cryptogenic
Lamellidea pusilla (Gould, 1847)	R	R	R, S	cryptogenic
PUPILLIDAE				
Gastrocopta pediculus (Shuttleworth, 1852)	B	R	B	cryptogenic
Nesopupa sp.	B		B	endemic/indigenous
Pupisoma orcula (Benson, 1850)	B	R	B	cryptogenic
PARTULIDAE				
Eua zebrina (Gould, 1847)		R		endemic
Samoana thurstoni (Cooke and Crampton, 1930)		R	S	endemic
SUBULINIDAE				
Allopeas clavulinum (Potiez and Michaud, 1838)	R	R	B, S	alien
Allopeas gracile (Hutton, 1834)	B	R	S	alien
Lamellaxis micra (d'Orbigny, 1835)	F	R	S	alien
Opeas hannense (Rang, 1831)	B	R	B, S	alien
Paropeas achatinaceum (Pfeiffer, 1846)	R	R	B, S	alien
Subulina octona (Bruguière, 1789)	R	R	R, S	alien
ACHATINIDAE				
Achatina fulica Bowdich, 1822	R			alien
SPIRAXIDAE				
Euglandina rosea (Férussac, 1821)	R			alien
STREPTAXIDAE				
Gulella bicolor (Hutton, 1834)	B	R	B, S	alien
Streptostele musaecola (Morelet, 1860)	R	R	S	alien
RHYTIDIDAE				
Ouagapia gradata (Gould, 1846)	R	R		indigenous
ENDODONTIDAE				
Minidonta manuaensis Solem, 1976	R		R	endemic
CHAROPIDAE				
Discocharopa aperta (Möllendorff, 1888)	R		R	indigenous
Sinployea clausa Solem, 1983	R			endemic
Sinployea allecta tauensis Solem, 1983	R			endemic

(continued)

Table 1. (continued)

Family/species	Ta‘ū	Ofu	Olosega	Status
SUCCINEIDAE				
Succinea manuana Gould, 1846	R	R	B, S	endemic
HELICARIONIDAE				
Coneuplecta microconus (Mousson, 1865)	B			indigenous
Diastole schmeltziana (Mousson, 1865)[c]	R	R	S	probably endemic
Liardetia samoensis (Mousson, 1865)	R	R	B, S	indigenous
Ovachlamys fulgens (Gude, 1900)			S	alien
BRADYBAENIDAE				
Bradybaena similaris (Rang, 1831)		R		alien

[a] The records from Ta‘ū and Ofu are based on unidentified veronicellids that are here tentatively referred to *Vaginulus plebeius*.

[b] New combination. Originally described in *Plecotrema* Adams and Adams, 1854 (see also Hubendick, 1956). Plectrema now a synonym of *Laemodonta* Philippi, 1846 (see Cowie *et al.*, 1995).

[c] A possibly undescribed species of *Diastole* was found at high elevations on all islands (e.g., Cowie, 2001a). It may, however, be just a variant of *Diastole schmeltziana* and is not listed separately, pending further research.

Manu‘a so far undertaken. Nevertheless, the absence of certain species, especially more generally widespread species, from one or more of the islands may well reflect a need for additional work rather than real absence. The neighboring islands of Ofu and Olosega have 24 species in common, yet these islands both share 28 species with more distant Ta‘ū. Ta‘ū, the largest and highest (but youngest–Keating, 1992) island, has 40 species; Ofu, slightly larger in area than Olosega, but also slightly lower, has 32; and Olosega, smallest in area but intermediate in elevation, has 30. Ta‘ū has the greatest number of native species (24); Ofu has 18; Olosega has 16. Although these numbers appear to reflect a clear species-area relationship, the determinants of species richness on islands are complex (Cowie, 1996a) and certainly three islands, even with complete data, are insufficient to detect large-scale trends or to confirm theoretical predictions (Cowie, 1996b). Patterns of distributions among the Manu‘a Islands may reflect a combination of incomplete sampling of the islands' faunas, randomness in the natural construction of those faunas, and the influence of other factors such as elevation and habitat diversity, all superimposed on an underlying species-area relationship.

The low level of endemism probably reflects the short distances between the three Manu‘a Islands as well as the relatively short distance from the larger islands of the Samoan archipelago. In addition, endemism among native Samoan land snail species as a whole is relatively low (63%; Cowie, 1998), compared for instance to the level in the Hawaiian fauna (over 99%; Cowie, 1996a). Less than one fourth of the species of Tutuila, the probable source of most of the Manu‘a species, are endemic to Tutuila (Cowie, 1998; Cowie and Cook, 2001). Most of the non-endemic native Samoan species are also found in Fiji, Tonga, and neighboring areas, and indeed most of the native (but not endemic) species of Manu‘a are distributed through the Samoan archipelago and westwards; some are more widespread Pacific species.

Many of the previously reported native species of the Manu‘a Islands (Cowie, 1998) were detected during the present survey of Olosega and recent surveys of Ta‘ū and Ofu (Cowie and Cook, 1999, 2001; Cowie, 2001a). However, among the species of Ta‘ū and Ofu, native species are declining while alien species are increasing in distribution and abundance (Cowie, 2001a). Because so few of the species recorded from Olosega had been reported prior to the present study, it is not possible to say for most of them whether they are declining or increasing. Nevertheless, the two endodontoids *(Minidonta manuaensis, Discocharopa aperta)* probably declined long ago because when they were first reported from Olosega, as dead shells (Solem, 1976, 1983), they were already considered extinct (see Cowie, 2001a). Perhaps they were never particularly abundant or widely distributed. Similarly, the partulid tree snail *Samoana thurstoni*, never previously reported from Olosega and the only partulid known from the island, is extremely rare on the island, although apparently distributed over a fairly wide elevational range from at least 300 m to 500 m. Its absence from previous records of land snails on Olosega may be because no one had searched for snails at these elevations on the island. It is similarly rare on Ofu, but known from a similar elevational range of 322 m to 491 m (the summit) (Cowie and Cook, 1999, 2001). Most partulids are single island endemics, but Olosega and Ofu are very close to each other, lie within the same reef on a single platform, and are the remnants of a single volcano (Wingert, 1981; Keating, 1992). It is thus not surprising to find the same partulid species on both islands. Similarly, another Samoan partulid, *Eua zebrina*, was recently discovered on Ofu (Cowie and Cook, 1999, 2001) although it was previously considered a Tutuila endemic. The tree snails of the family Partulidae, to which *S. thurstoni* and *E. zebrina* belong, are considered the "flagships" of invertebrate conservation in the Pacific (Cowie and Cook, 2001). Partulids are especially vulnerable to the suite of threats faced by native snails on Pacific islands, perhaps because of their long life-cycle and slow reproductive rate (Cowie, 1992). Despite the fact that *S. thurstoni* is now known from two islands it remains under serious threat. Because the population on Olosega is much less accessible than that on Ofu, the Olosega population is of especial significance for the conservation of this rare species. No partulids have been recorded on Ta‘ū despite intensive survey work extending to the summit of the island (Cowie and Cook, 1999, 2001). They may indeed be absent from that island, the youngest of the main Samoan islands (Keating, 1992), perhaps simply because they have not yet chanced to reach it.

While many of the native species may be declining, alien species, especially subulinids, are probably increasing on Olosega, as on the other Manu‘a Islands (Cowie, 2001a). Ten alien species were recorded on Olosega during the 2001 survey (Table 1) and six of these were subulinids. Of these six subulinids, four had been previously collected on the island [*Allopeas clavulinum* (Potiez and Michaud, 1838), *Opeas hannense* (Rang, 1831), *Paropeas achatinaceum* (Pfeiffer, 1846), *Subulina octona* (Bruguière, 1789)]. *Allopeas clavulinum* and *O. hannense* have never been especially common (evidenced by the extent of collections in the Bishop Museum) and very few individuals were found. However, the other two species are the most widespread and abundant alien snails on Pacific islands (Cowie, 2000, 2001a, 2002). The fifth subulinid, *Allopeas gracile* (Hutton, 1834), has been considered the most widespread land snail species in the world (Pilsbry, 1906-1907; Deisler and Abbott, 1984). It was once relatively common on Ofu (Kirch, 1993) and appears to have been introduced widely in the Pacific prior to western exploration (Christensen and Kirch, 1981, 1986), unlike the other subulinids, which are more recent introductions. However, *A. gracile* is now rarely encountered except as a fossil/subfossil and only a single shell was found during the Olosega survey. The sixth subulinid, *Lamellaxis micra* (d'Orbigny, 1835), has never been common and has only been recorded from scattered locations in the Pacific (Cowie, 2000, 2002); only a single shell was found.

The absence of *Achatina fulica* and *Euglandina rosea* from Olosega and Ofu (Cowie and Cook, 2001) is encouraging. *Euglandina rosea* has been widely introduced as a putative biological control agent of *A. fulica* (Griffiths *et al.*, 1993; Civeyrel and Simberloff, 1996; Cowie, 2001b) but nowhere has successful control been demonstrated, and *E. rosea* has been heavily implicated in the decline and extinction of native land snail species in the Pacific, notably Partulidae (Murray *et al.*, 1989; Cowie, 1992) and Achatinellinae (Hadfield, 1986; Hadfield *et al.*, 1993). *Achatina fulica* and *Euglandina rosea* are both present on Ta‘ū (Cowie, 1998) but we hope they can continue to be kept out of Ofu and Olosega.

The absence of *Lamellidea oblonga* from the survey collections may reflect difficulty in distinguishing it from *Lamellidea pusilla* (Gould, 1847); however, all the material collected in 2001 was referred to *L. pusilla* relatively confidently.

There remain a number of taxonomic difficulties that render some of the present identifications somewhat tentative. Cowie and Cook (1999) and Cowie (2001a) may have been incorrect in not listing *Melampus luteus* but listing *M. castaneus* from Ta‘ū and Ofu (and Tutuila). Unidentified ellobiids are present in the Bishop Museum collections and may represent additional species. Identification of veronicellid slugs also remains difficult but is important because of their increasing abundance and spread throughout much of the Pacific, and their possible ecological impacts. Additional taxonomic work on other groups unstudied in the Pacific since the early twentieth century or before is necessary if identification of some of these difficult-to-identify species is to be made more rigorous.

The native land snail fauna of the islands of the Pacific (excluding New Guinea) probably numbers around 4,000 species and exhibits high levels of single island or single archipelago endemism (Cowie, 1996b, 2000). However, this number is only an educated guess, as many islands remain poorly known. The alien land snail fauna contains far fewer species, probably between 100 and 200, with many of these widely distributed (Cowie, 2000, 2002). The island by island distributions of many of these aliens have not been well documented. The present survey of the relatively accessible Samoan island of Olosega underlines the need for much more detailed survey work and suggests that the land snail faunas of other more isolated and less studied islands or island groups in the Pacific are probably extremely poorly known. Many of the native species are declining and being replaced by widespread aliens, but the extent to which this is happening remains unknown on most islands. As a fundamental step in the conservation of these native Pacific island species, much more survey work, especially on the more remote and under-studied islands, is essential to provide the necessary baseline biodiversity information.

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An endemic radiation of *Trituba* (Mollusca, Gastropoda) on the North Atlantic seamounts

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Abstract: Ten species of the genus *Trituba* are recognized on the seamounts of the North Atlantic south of the Azores, and interpreted as the product of a single radiation in a taxon which has had a relict distribution since the Miocene. The species are *Trituba superstes* (Bouchet and Fechter, 1981) and *T. incredita* n. sp. from Meteor bank; *T. anelpistos* (Bouchet and Fechter, 1981) from Meteor, Hyères, and Irving banks; *Trituba recurvata* n. sp. from Hyères bank; *T. constricta* n. sp., *T. fallax* n. sp., and *T. additicia* n. sp. from Hyères and Irving banks; *T. lima* n. sp. from Irving bank; *T. elatissima* n. sp. from Plato and Atlantis banks; and *T. hirta* n. sp. from Atlantis bank. The level of bank-to-bank endemism is high, with four species endemic to a single bank. This indicates that the distances, in the order of magnitude of 100 to 200 km, between the banks are barriers for larvae and egg capsules of these species of *Trituba*, which are inferred to have an intracapsular larval development. There is very much difference in the success of the different species, as reflected by their relative abundances, ranging from the 64 specimens and over 500 shells collected of *T. constricta* to the 4 shells of *T. additicia*; some of the rarer species could be very prone to extinction or may even be extinct. The diversification into a set of species with different depth ranges and morphologies is interpreted as a factor that will enhance the probability of survivorship in the lineage. The common species suffer important predation pressure, presumably from a muricid gastropod, and one third to two thirds of the adult shells are drilled in the large populations of *T. constricta*.

Key Words: Triforidae, endemism, survivorship, seamount, dispersal

The seamounts of the Meteor group, situated approximately 600 km south of the Azores and 1100 km west of the Canaries, hold one of the most isolated benthic biota in the North Atlantic. To date, there is only very fragmented knowledge of this fauna. The only previous museum material was that collected by R/V Meteor cruise 9C in 1967. The Seamount 2 expedition visited the banks in January-February 1993 and yielded a large amount of material which is currently under study.

This paper deals with a group which has been known hitherto from the two species described by Bouchet and Fechter (1981) and from a fragmentary shell figured by Bouchet and Warén (1993). The Seamount 2 material contains a large number of specimens, many of which were live-collected. There are several closely related species, either sympatric or allopatric from bank-to-bank, making it possible to find one to four sympatric species within a particular sample, and up to five different species on a particular seamount.

MATERIAL AND METHODS

The Seamount expeditions were directed to general collecting of the benthic fauna with views to understand the colonization of remote sites by the benthos, at the initiative of Philippe Bouchet (of Muséum National d'Histoire Naturelle, Paris, hereafter MNHN). Seamount 2 (Fig. 1) was conducted in January/February 1993 by the author and visited the Great Meteor bank, Hyères, Irving (also named Cruiser), Plato, Atlantis, and Tyro seamounts (69 dredge hauls and 16 beam trawl operations shallower than 1000 m). The material was sorted to the species level and

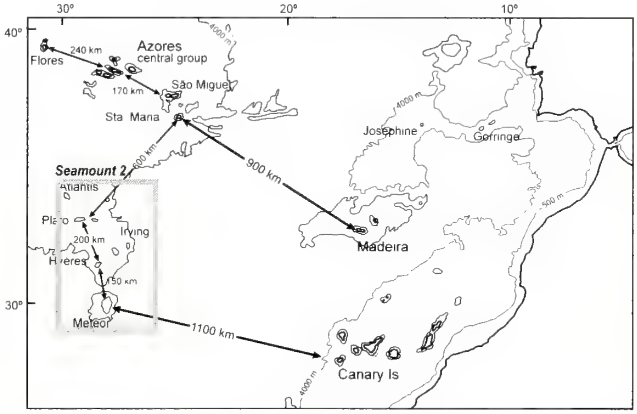

Fig. 1. Map showing the location of the Northeast Atlantic seamounts and their distances to the mainland.

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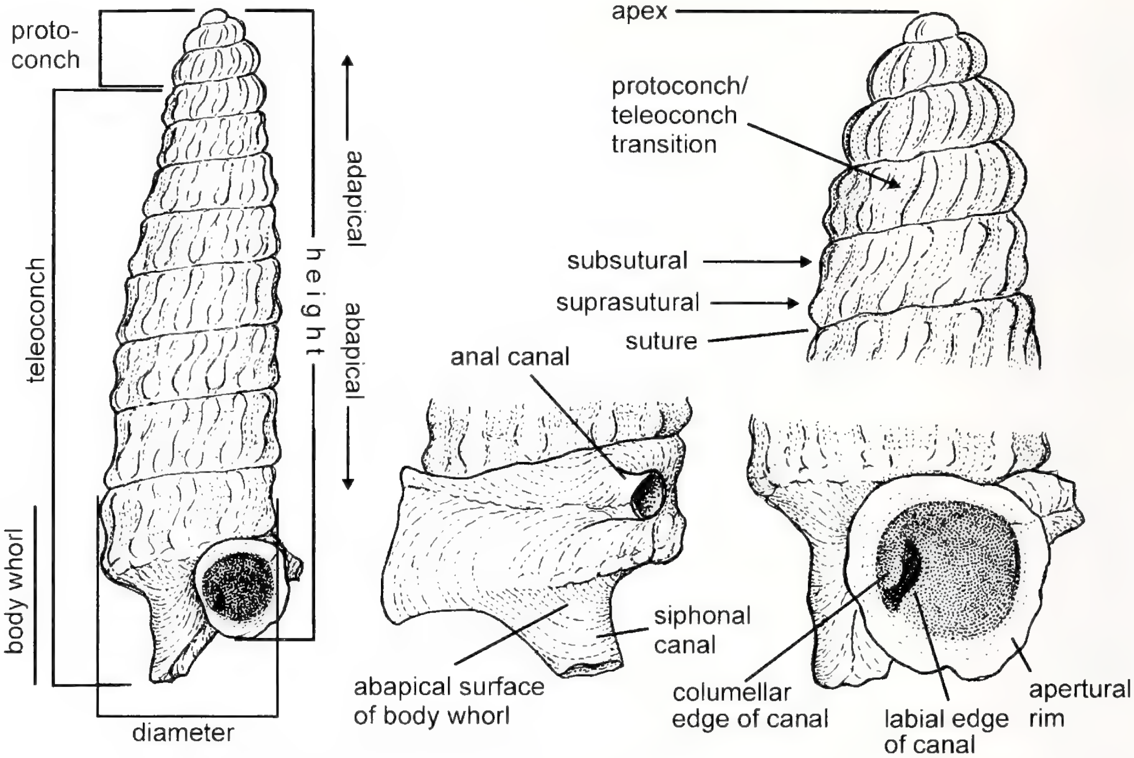

Fig. 2. The shell of a *Trituba* species, showing some descriptive terms used in this paper.

deposited in the malacological collection of MNHN.

Most of the collected material consisted of shells, and these were taken into account in the mollusc counts. The coarse fractions, usually above 10 mm, were mostly sorted on board to phyla, then sorted to species level in the lab. The finer fractions were preserved as whole on board, and later sieved on 5 mm, 2 mm, 1 mm, 0.5 mm, and 0.3 mm sieves, and sorted under a stereomicroscope. Drawings of living animals were prepared wherever possible, and include one entry for *Trituba*. The specimens and shells of *Trituba* were collected in dredge hauls containing large quantities of geodid and other sponges, on which these gastropods may feed. The coordinates and depths of the relevant hauls are indicated in Table 1.

Heights of shells of *Trituba* (Fig. 2) were measured from the apex to the lower edge of the lip. The maximum diameter was measured on the penultimate whorl so as to leave out the peristome features. Juvenile specimens had a flat abapical surface and lacked the adult apertural features, but were usually easy to assign to a particular species by assembling growth series and comparing protoconch characters and teleoconch sculpture.

Important and stable characters, well correlated with independent teleoconch characters, were found in the shape and sculpture of the protoconch. The number of whorls could not be determined with very much precision, because there was no physical limit and a very gradual transition to the teleoconch; the demarcation was indicated by the change in sculpture, where the ribbed pattern was replaced by a pattern of knobs, but this is not clear cut in species where the teleoconch was also ribbed. The profile of the protoconch also provided informative characters, including whether the apex was sunken in the next whorl or protruding, and if the later protoconch whorls were swollen so as to depart from the general profile of the spire or conformed to the high conical template.

On the teleoconch, characters were derived from the sculpture, the general profile, and the apertural features. The profile of the body whorl may be constricted, that is with a diameter smaller than would be expected from the geometrical continuation of the previous spire whorls. There were two canals in addition to the aperture, which were usually closed and tubular in the adults, one siphonal (anterior in life position) and another, anal, opposite to it. The length and curvature of the anal canal was an informative feature. The morphology inside the siphonal canal i.e. how the columellar edge of the canal related to the opposite edge, has been shown as important by Marshall (1977). Among the species studied herein, this character was used for discriminating the two Meteor bank species described by Bouchet and Fechter (1981), but was not very helpful elsewhere. The abbreviations used for the material

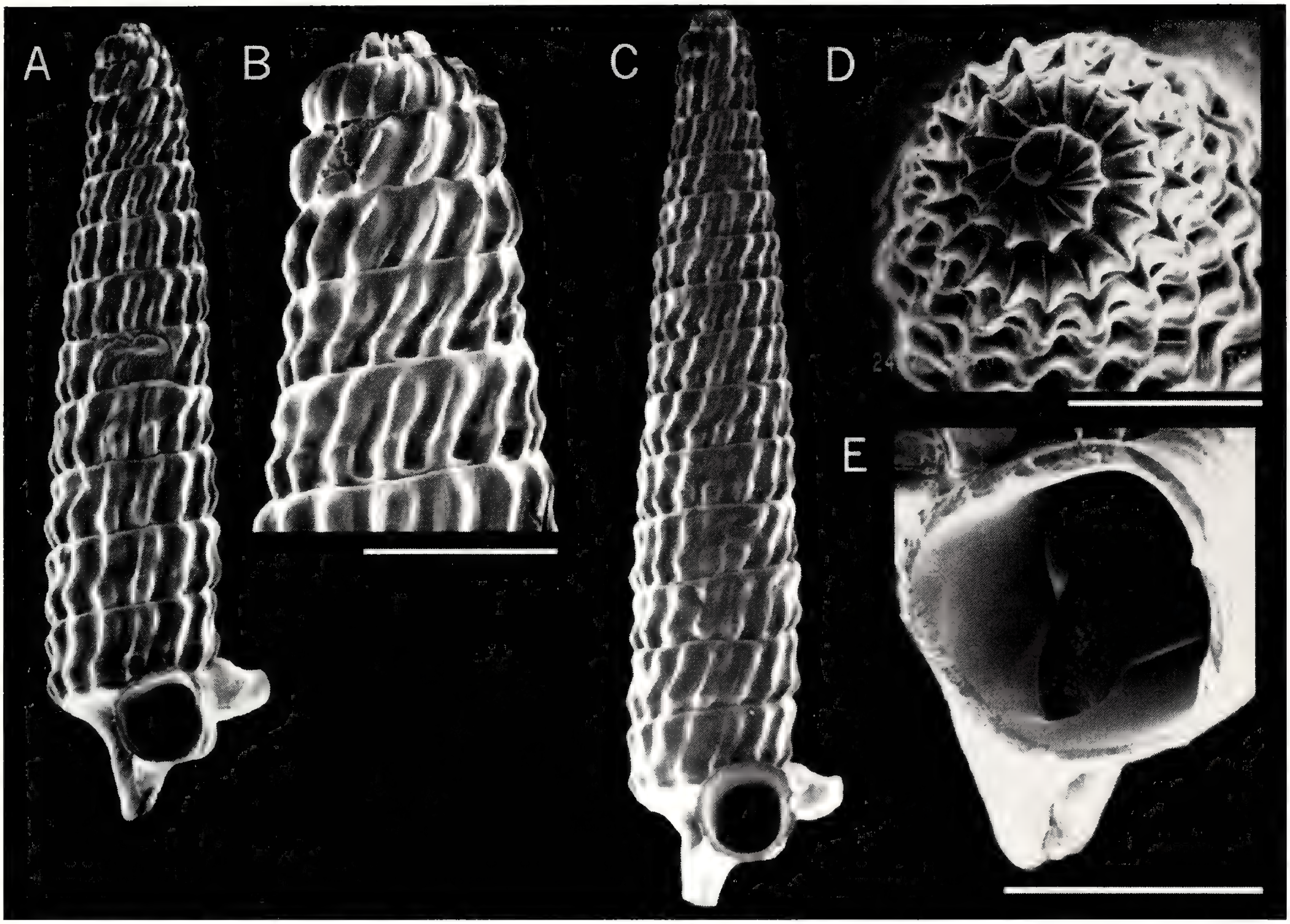

Fig. 3. *Trituba superstes* (Bouchet and Fechter, 1981) from Meteor bank, DW152. **A.** Shell (4.9 mm long). **B.** Protoconch, same specimen as A. **C.** Shell (6.7 mm long). **D.** Apical view of protoconch of another specimen. **E.** Oblique view of the aperture, to show the widely separated edges of siphonal canal, same specimen as A. Scale bars = 500 μm.

examined are: sh, shell(s); spm, live-collected specimen(s); sta, station number of research vessel.

SYSTEMATICS

Genus *Trituba* Jousseaume, 1884

Remarks

The genus considered in this paper has been hitherto known as "*Triforis* Deshayes, 1834." Bouchet and Marshall (in press) has requested ICZN to confirm *Triforis* "Deshayes, 1834" as an incorrect subsequent spelling of *Triphora* Blainville, 1828, so that the valid generic name for the species described herein should be *Trituba* Jousseaume, 1884 (Type species by original designation: *Triforis bitubulatus* Baudon, 1856, a fossil from the Eocene of France).

The genus was placed in the family Triforidae Jousseaume, 1884, and superfamily Cerithiopsoidea by Marshall (1980).

Trituba superstes (Bouchet and Fechter, 1981)
(Figs. 3, 4)

Type material

Holotype (sh., 4.9 x 1.4 mm) and 2 paratypes (sh.) in Zoologische Staatssammlung, München; 1 paratype (sh.) in MNHN; all from "Meteor" cruise 9c sta. 172.

Type locality

Meteor bank, 29°48'N - 28°23'W, 300-310 m.

Material examined

Meteor bank, DW143: 1 sh. (3.9 x 1.1 mm); DW152: 11 spm. (7 adult, 4.9 x 1.2 to 6.9 x 1.4 mm) and 31 sh. (18 adult).

Table 1. List of sampling stations of Seamount 2 cruise where *Trituba* spp. were collected.

Meteor bank			
DE 140	30°01.1'N	28°27.7'W	308 m
DW 143	30°09.9'N	28°28.1'W	330 m
DW 152	30°02.0'N	28°22.1'W	470 m
DW 166	29°36.0'N	28°22.8'W	575 m
DW 172	30°05.1'N	28°41.5'W	455 m
DW 179	30°00.6'N	28°42.3'W	730 m
Hyères bank			
DW 182	31°23.2'N	28°53.5'W	480 m
DW 184	31°24.4'N	28°52.3'W	705 m
DW 186	31°26.1'N	28°51.8'W	1520 m
DW 188	31°30.0'N	28°59.5'W	310 m
DW 190	31°29.0'N	29°00.0'W	750 m
DW 192	31°27.9'N	28°59.1'W	750 m
DW200	31°19.1'N	28°36.0'W	1060 m
DW202	31°16.5'N	28°43.1'W	640 m
DW203	31°09.5'N	28°43.5'W	845 m
Irving bank			
DW205	32°01.1'N	27°57.2'W	348 m
DW209	31°59.2'N	27°55.9'W	460 m
DW215	31°53.6'N	28°02.9'W	275 m
DW216	31°53.7'N	28°03.0'W	270 m
DW225	32°08.6'N	28°10.7'W	1035 m
DW231	32°01.5'N	27°54.5'W	745 m
DW237	32°15.9'N	27°31.8'W	670 m
DW238	32°17.3'N	27°32.3'W	890 m
Plato bank			
DW240	33°12.3'N	29°01.9'W	565 m
DW241	33°11.9'N	28°59.3'W	695 m
DW242	33°11.8'N	28°57.0'W	710 m
DW247	33°13.7'N	29°35.3'W	580 m
DW248	33°13.6'N	29°32.5'W	735 m
Atlantis bank			
DW255	34°04.9'N	30°15.3'W	340 m
DW258	33°59.8'N	30°12.1'W	420 m
DW263	34°25.9'N	30°32.5'W	610 m
DW274	34°05.1'N	30°13.6'W	280 m

Redescription

Shell up to 6.8 x 1.4 mm, turriculate, solid, white, with 12-15 whorls. Protoconch ca. 2.5-3 whorls, with maximum diameter 0.75 mm, the nucleus quite sunken in the following whorl, resulting in a very blunt apex; protoconch whorls strongly and evenly convex, sculptured with strong and elevated, sharp, widely spaced ribs starting on the very first whorl, slightly oblique on the first and second whorls, still more oblique on the third.

Teleoconch whorls sculptured with quite strong, slightly oblique ribs on which there is a subsutural and a suprasutural bulge, separated by a broad depression; the suprasutural bulges bordered adapically by a faint spiral line. Body whorl hardly narrowing; its abapical surface smooth and circled by a faint keel on which the ribs terminate.

Aperture with a continuous, moderately flaring peristome. Siphonal canal moderately long, narrowing towards outer opening, inside with columellar and labial edges set widely apart. Anal canal similar in size and shape to the siphonal, moderately curved, pointing sidewards.

Remarks

Trituba superstes was not found outside Meteor bank. Specimens from Hyères bank with this kind of teleoconch sculpture had a more protruding first protoconch whorl and thus lacked the very characteristic blunt apex of *T. superstes*; they are treated as a different species, *Trituba fallax*.

A living specimen of this species was observed from DW152 (Fig. 4). The head-foot was tiny in comparison to the shell, but nevertheless the animal managed to crawl around. The mantle edge remained concealed inside the aperture at the time of observation. The cephalic tentacles were tapered, with blunt ends, and set close together so as to form a V-shaped structure as in *Cerithiopsis*. The foot was truncated anteriorly, tapered posteriorly, and bore a longitudinal median groove on the sole, extending from the propodium to the metapodium. On the sides, there was also a shallow groove slightly above the edge of the sole. A pedal gland was visible by transparency in the posterior part of the foot, beneath the operculum. The head-foot was entirely white.

Trituba anelpistos (Bouchet and Fechter, 1981)
(Fig. 5)

Type material

Holotype (sh., 4.4 x 1.3 mm) in Zoologische Staatssammlung, München, from "Meteor" cruise 9c sta. 172.

Type locality

Meteor bank, 29°48'N - 28°23'W, 300-310 m.

Material examined

Meteor bank, DE140: 1 sh. (4.3 x 1.2 mm); DW143: 1 sh.; DW152: 21 spm. (17 adult, 3.1 x 1.0 to 5.4 x 1.3 mm) and 49 sh. (38 adult); Hyères bank, DW182: 15 sh. (adult, 3.1 x 0.9 to 4.8 x 1.4 mm), DW188: 1 spm. (4.3 x 1.1 mm) and 2 sh.; Irving bank, DW237: 3 spm. (adult, 3.7 x 1 to 5.1 x 1.3 mm) and 23 sh. (21 adult).

Redescription

Shell up to 5.4 x 1.3 mm, turriculate, solid, white, with 10-13 whorls. Protoconch ca. 2.5-3 whorls, with maximum diameter 0.6 mm, the nucleus quite protruding; protoconch whorls convex, sculptured with strong, thick ribs, almost axial on the first and second whorl, more oblique on the third whorl.

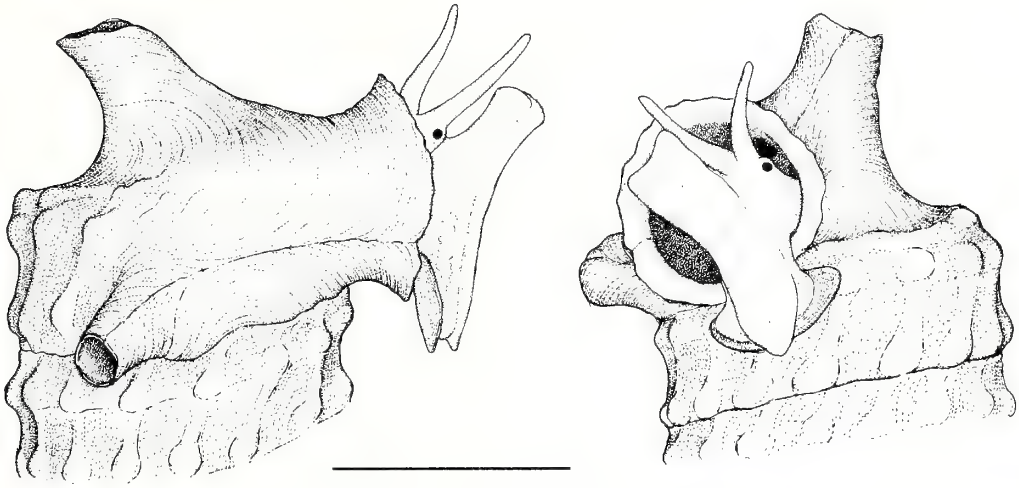

Fig. 4. *Trituba superstes*, drawing of a living animal from Meteor bank, DW152. Scale bar = 500 µm.

Teleoconch whorls sculptured with quite strong, blunt, slightly oblique ribs, very slightly swollen towards their subsutural and suprasutural parts, and depressed in between; the suprasutural swells are more distinct and bordered adapically by a very faint spiral line. Body whorl slightly narrowing, with ribs attenuated or absent; its abapical surface smooth and circled by a strong keel on which the ribs, if any, terminate.

Aperture with a continuous, moderately flaring peristome. Siphonal canal moderately long, narrowing towards outer opening, inside with columellar and labial edges coming very close together. Anal canal similar in size and shape to the siphonal, moderately curved, pointing sidewards.

Remarks

Specimens referable to *Tributa anelpistos* were found on Meteor, Hyères, and Irving banks. Specimens from Irving were smoother and had a very sharp keel on the body whorl, and also had a thicker (maximum diameter 0.75 mm) protoconch with less convex whorls. They also occurred deeper (670 m, see Fig. 14). Although some differentiation did occur, I did not find useful to formally name a subspecies.

Trituba fallax n. sp. from Hyères bank resembled *T. anelpistos* in having a heavily ribbed protoconch and a predominantly axial teleoconch sculpture, but was larger, had a non-constricted body whorl, a distinct spiral line bordering the suprasutural knobs on the ribs, and had smaller canals.

Trituba incredita Gofas, new species

(Fig. 6)

Type material

Holotype (spm., 6.2 x 1.4 mm) and paratypes, 1 spm. (adult) and 33 sh. (17 adult, largest 8.2 x 1.9 mm) from Seamount 2 sta. DW152.

Type locality

Meteor bank, 30°02.0'N - 28°22.1'W, 470 m.

Other material examined

Meteor bank, DW166, 1 sh. (8.8 x 2.0 mm without protoconch); DW172, 1 sh. (8.7 x 1.9 mm); DW179, 3 sh. (1 adult, 10.0 x 2.2 mm).

Description

Shell up to 10 x 2.2 mm, turriculate, solid, white, with 12-18 whorls. Protoconch ca. 3 whorls, the nucleus moderately protruding, with a pupoid profile, inflated so as to depart slightly from the general spire profile; protoconch whorls moderately convex, less so along the subsutural portion, sculptured with numerous, delicate, evenly spaced, oblique and flexuous ribs.

Teleoconch whorls sculptured with strong subsutural and suprasutural knobs, arranged in two spiral rows which are offset from each other so as to form oblique axial ribs; the suprasutural knobs stronger on the first teleoconch whorl and bordered adapically by a definite spiral line. Body whorl hardly narrowing; its abapical surface smooth and circled by a quite strong keel on which the ribs terminate.

Aperture with a continuous, flaring peristome. Siphonal canal moderately long, parallel sided, inside with columellar and labial edges coming moderately close together. Anal canal smaller than the siphonal, moderately curved, pointing sidewards.

Etymology

The name alludes to the shipboard party's scepticism, at the beginning of the expedition, about finding more than one species of this genus.

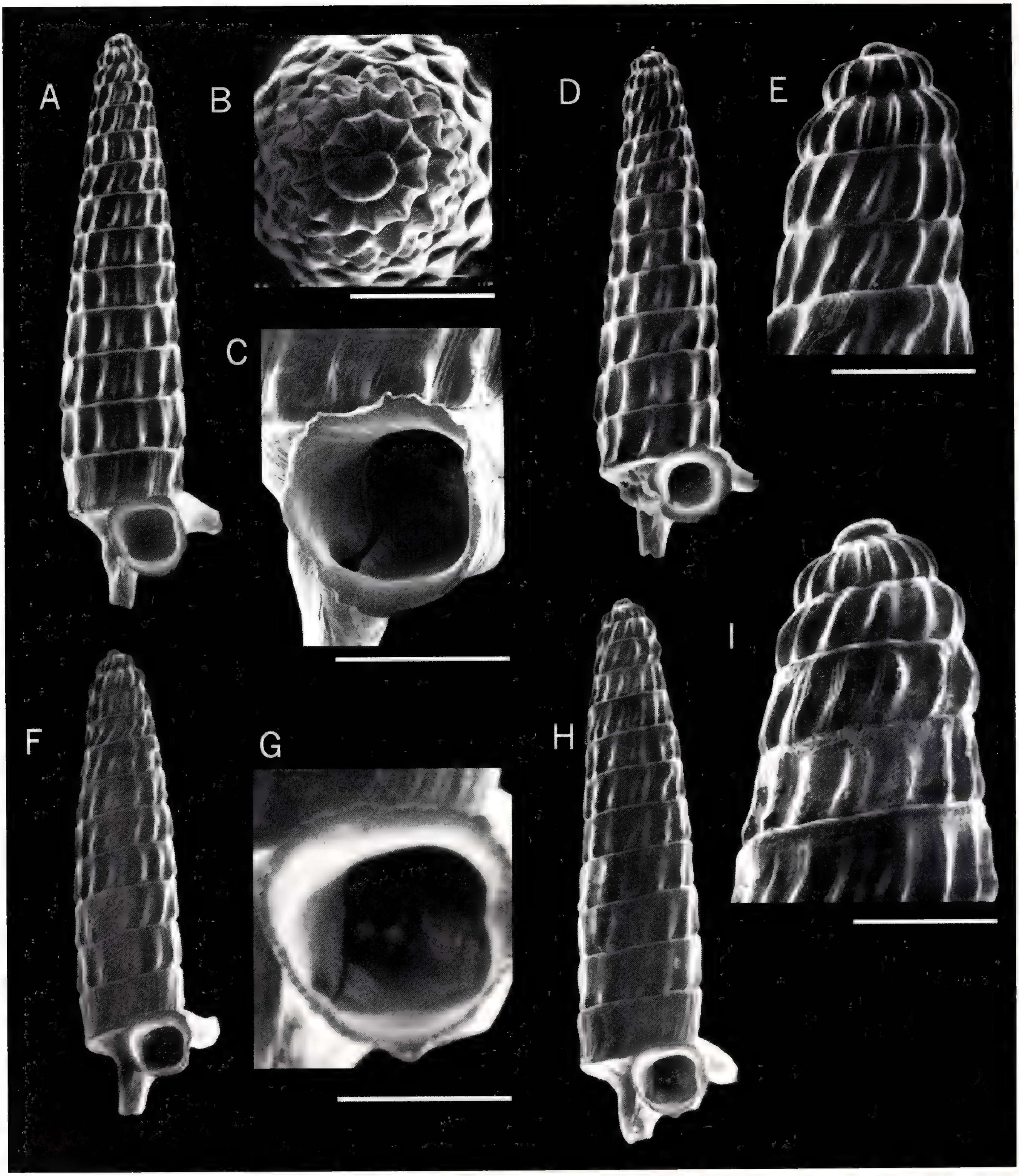

Fig. 5. *Trituba anelpistos* (Bouchet and Fechter, 1981). **A.** Shell from Meteor bank, DW152 (5.4 mm long). **B.** Apical view of protoconch. **C.** Aperture, to show the closely set edges of siphonal canal, same specimen as A. **D.** Shell from Hyères bank, DW188 (4.3 mm long). **E.** Protoconch, same specimen as D. **F, H.** Specimens from Irving bank, DW237 (4.2 and 5.1 mm long respectively). **G.** Aperture, same specimen as H. **I.** Protoconch, same specimen as H. Scale bars = 500 µm.

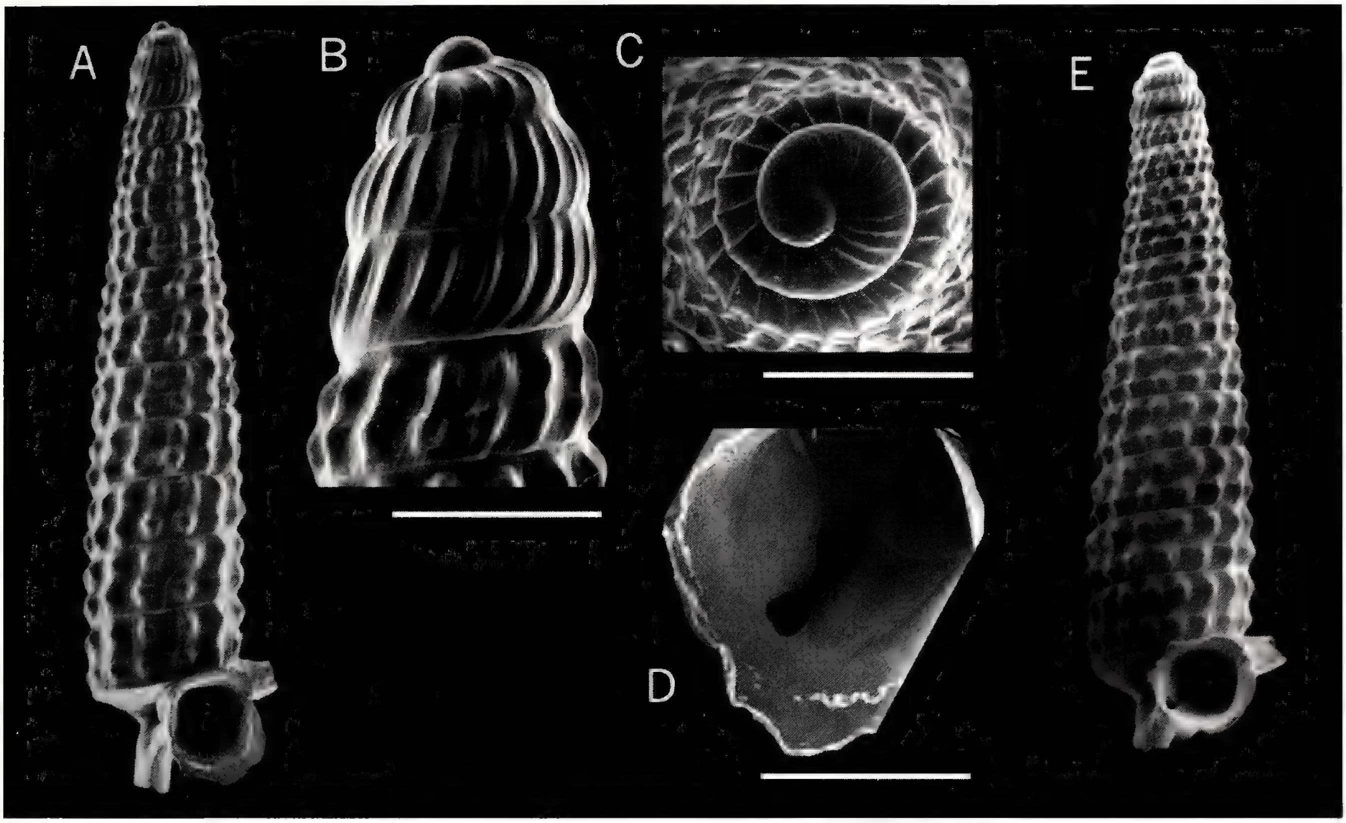

Fig. 6. *Trituba incredita* n. sp. **A.** Holotype from Meteor bank, DW152 (6.2 mm long). **B.** Protoconch of the holotype. **C.** Apical view of protoconch of another specimen. **D.** Oblique view of the aperture of the holotype, to show the inside of siphonal canal. **E.** Paratype from Meteor bank, DW 152 (5.6 mm long). Scale bars = 500 µm.

Remarks

This species differed from the two other Meteor bank species by the delicately sculptured, oblong protoconch and more cylindrical canal. The type of protoconch sculpture was shared with two species of Hyères bank and may indicate that they are related. *Trituba recurvata* was similar in most respects but differed in having a very long and curved anal canal. The morphs of *T. constricta* with the more accentuated sculpture looked quite similar as well, but the knobs from the two adjacent spiral rows tended to unite axially so as to form axial ribs; *T. constricta* also reached a larger size, and had a distinctly narrowing body whorl.

Trituba constricta Gofas, new species
(Fig. 7)

Type material

Holotype (spm., 9.4 x 2.1 mm) and paratypes, 10 spm. (9 adult) and 14 sh. (11 adult, 9.4 x 2.0 to 15.0 x 2.7 mm) from Seamount 2 sta. DW188.

Type locality

Hyères bank, 31°30.0'N - 28°59.5'W, 310 m.

Other material examined

Hyères bank, DW182: 3 spm. (juvenile) and 56 sh. (16 adult); DW184: 3 spm. (2 adult, 14.5 x 2.6 mm, 14.5 x 3.1 mm) and 30 sh. (28 adult, 13.0 x 2.7 to 19.0 x 3.2 mm, of which 20 drilled by gastropod predator); DW186: 5 sh. (broken, very smooth); DW188: 43 spm. (33 adult, 8.5 x 1.9 to 15.1 x 2.8 mm) and 336 sh. (248 adult, 9.0 x 1.9 to 15.5 x 2.8 mm, of which 80 drilled by gastropod predator); DW190: 3 spm. (adult, 11.7 x 2.5 to 13.9 x 2.8 mm) and 1 sh. (8.9 x 2.1 mm); DW192: 4 spm. (3 adult, 8.9 x 2.0 to 10.2 x 2.1 mm) and 11 sh. (9 adult, 8.9 x 2.0 to 10.7 x 2.4 mm); DW202: 5 sh. (adult, 14.0 x 2.6 to 18.3 x 3.0 mm); DW203: 8 spm. (6 adult, 12.5 x 2.5 to 14.0 x 2.9 mm) and 78 sh. (52 adult, 10.0 x 2.5 to 16.9 x 3.0 mm) Irving bank, DW205: 1 sh. (8.0 x 1.9 mm); DW209: 1 spm. (6.9 x 1.8 mm) and 13 sh. (12 adult, 8.0 x 1.9 to 10.8 x 2.5 mm).

Description

Shell up to 19 x 3.2 mm, turriculate, solid, white, with 20-22 whorls. Protoconch ca. 3-3.5 whorls, with maximum diameter 0.7 mm, the nucleus quite protruding; first protoconch whorl with maximum convexity along suprasutural zone; the second whorl convex, with the suprasutural

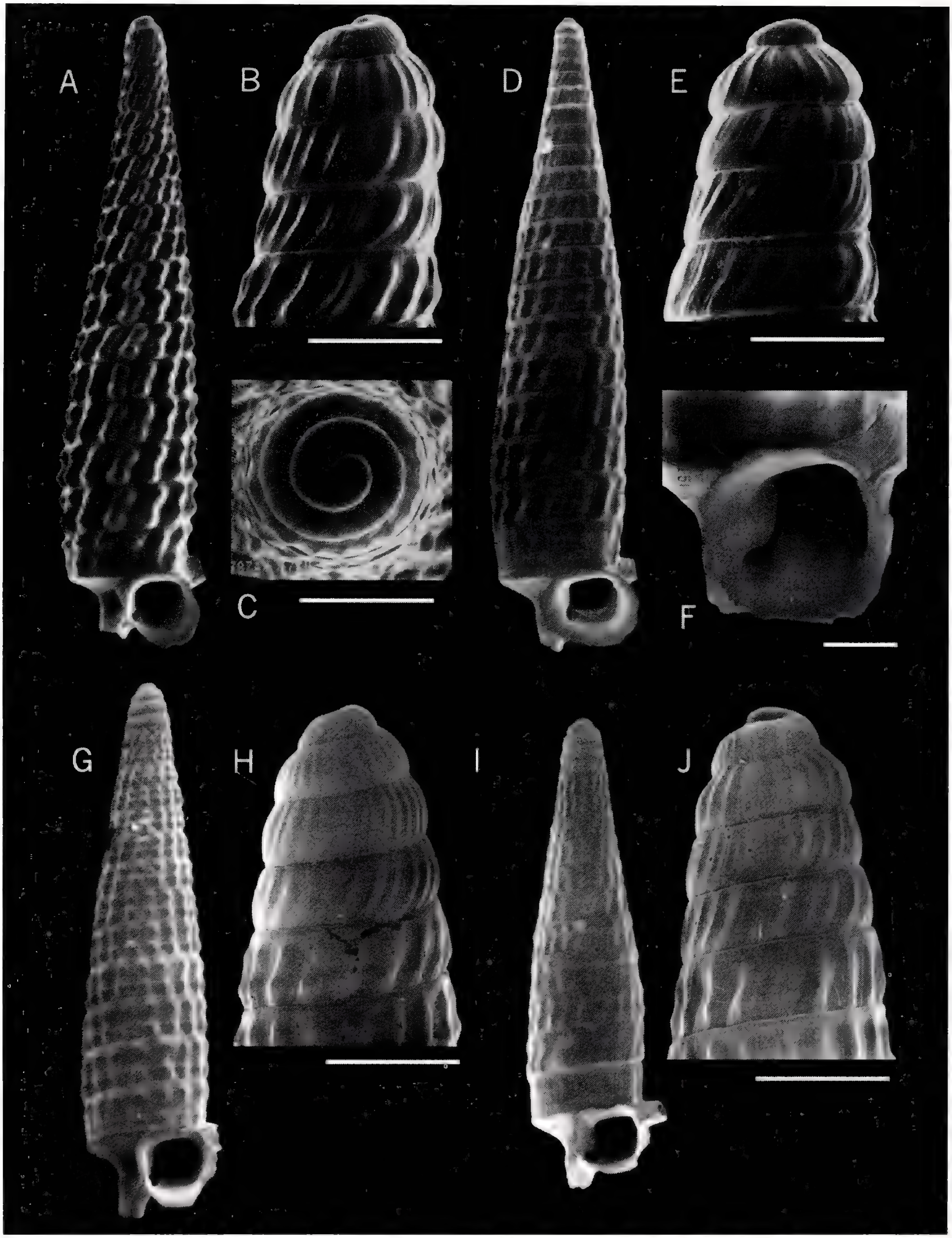

Fig. 7. *Trituba constricta* n. sp. **A.** Holotype from Hyères bank, DW188 (9.4 mm long). **B.** Protoconch of the holotype. **C.** Apical view of protoconch of another specimen. **D.** Specimen from Hyères bank, DW 203, with attenuated sculpture (12.5 mm long). **E.** Protoconch, same specimen as D. **F.** Aperture or a paratype from DW188. **G.** Specimen from Irving bank, DW209 (7.9 mm long). **H.** Protoconch, same specimen as G. **I.** Another specimen from Irving bank, DW209, with very attenuated sculpture (6.9 mm long). **J.** Protoconch, same specimen as I. Scale bars = 500 μm.

portion slightly overhanging the following whorl; first protoconch whorl nearly smooth, the following sculptured with weak folds, nearly axial on the first whorl, more oblique on the second and third whorls.

Teleoconch whorls with a glossy surface, sculptured with slightly oblique ribs on which there are two variably developed bulges separated by a depression; the suprasutural bulges bordered adapically by a faint spiral line. Body whorl definitely constricted, with axial sculpture gradually becoming attenuated or disappearing; its abapical surface smooth and circled by a strong keel on which the ribs, if any, terminate. On some specimens, the abapical row of bulges continued on the body whorl as a faint additional keel.

Aperture with a continuous, flaring peristome. Siphonal canal very short, narrowing towards outer opening, inside with columellar and labial edges coming moderately close. Anal canal small and short, pointing sidewards.

Etymology

The name recalls the narrowing profile of the body whorl.

Remarks

This species was present in large numbers in samples from the broad depression on the NW upper slope of Hyères bank, where sponges were thriving. Specimens referable to this species were also collected on Irving bank. Its large size, very short canals, attenuated sculpture and narrowing body whorl made it unmistakable among the NE Atlantic seamount radiation. The protoconch morphology with delicate sculpture was shared with several species: *Trituba incredita*, of Meteor bank, was smaller, had more distinct beads on the teleoconch and did not narrow the body whorl so much; the sympatric *Trituba recurvata* differed in the same characters and in having a very long, reflected anal tube; *Trituba lima*, from Irving bank, was similar in size and profile and also had very short canals, but differed in having a rough teleoconch sculpture and one more protoconch whorl.

There is a distinct variation with depth on Hyères bank, where specimens from the shallower samples (300-600 m) were smaller (8.5 to 15.5 mm) and had more distinct bulges, which could almost be termed knobs, on the ribs, whereas those from the deeper samples were larger (up to 19 mm) and tended to have attenuated sculpture. However, every transition could be seen in the large samples examined, and there was no other character correlated with this variation which could indicate that more than one species was involved.

The few specimens collected from Irving bank (Fig. 7, G-J) differed in being somewhat more stout and in that the knobs on spire teleoconch whorls were aligned more or less parallel to the main axis, rather than oblique. However, the other characters, including the protoconch sculpture and the constriction of the body whorl, were similar, so that they were tentatively considered as conspecific. There was also a variation in the intensity of sculpture, the most extreme specimens being quite smooth.

Trituba fallax Gofas, new species

(Fig. 8)

Type material

Holotype (spm., 8.8 x 1.8 mm) and paratypes, 7 spm. (5 adult, 5.8 x 1.5 to 8.8 x 1.8 mm) and 10 sh. (adult, 6.5 x 1.6 to 9.9 x 1.9 mm) from Seamount 2 sta. DW188.

Type locality

Hyères bank, 31°30.0'N - 28°59.5'W, 310 m.

Other material examined

Hyères bank, DW182: 65 sh. (15 adult, 6.6 x 1.7 to 11.8 x 2.5 mm); DW188: 38 sh. (36 adult, 6.8 x 1.6 to 10.4 x 2.2 mm); DW192: 16 sh. (10 adult, 6.6 x 1.6 to 12.2 x 2.4 mm); Irving bank, DW205: 2 spm. (1 adult, 15.2 x 2.6 mm) and 1 sh.; DW209: 1 spm. (10.5 x 2.1 mm) and 2 sh. (broken); DW215: 1 sh. (9.4 x 2.0 mm, broken apex); DW216: 1 sh. (8.8 x 1.9 mm); DW231: 1 fragment.

Description

Shell up to 12.2 x 2.4 mm, turriculate, solid, white, with 14-20 whorls. Protoconch ca. 2.5-3 whorls, with maximum diameter 0.7 mm; the nucleus quite protruding and the whorls regularly increasing in diameter; protoconch whorls convex, sculptured with strong, thick ribs, almost axial on the first whorl, then more oblique.

Teleoconch whorls with a glossy surface, sculptured with quite strong, oblique ribs, swollen towards their subsutural and suprasutural parts, and depressed in between; the subsutural end with definite knobs in the early whorls, less so in the later ones; the suprasutural knobs distinct throughout and bordered adapically by a definite spiral line. Body whorl not narrowing; its abapical surface smooth and circled by a strong keel on which the ribs terminate.

Aperture with a continuous, moderately flaring peristome. Siphonal canal short, hardly narrowing towards outer opening, inside with columellar and labial edges coming very close together. Anal canal short, pointing sidewards.

Etymology

The name alludes to the misleading similarities with a large *Trituba anelpistos*.

Remarks

Trituba fallax resembled *Trituba anelpistos* in the general pattern of sculpture of the protoconch and

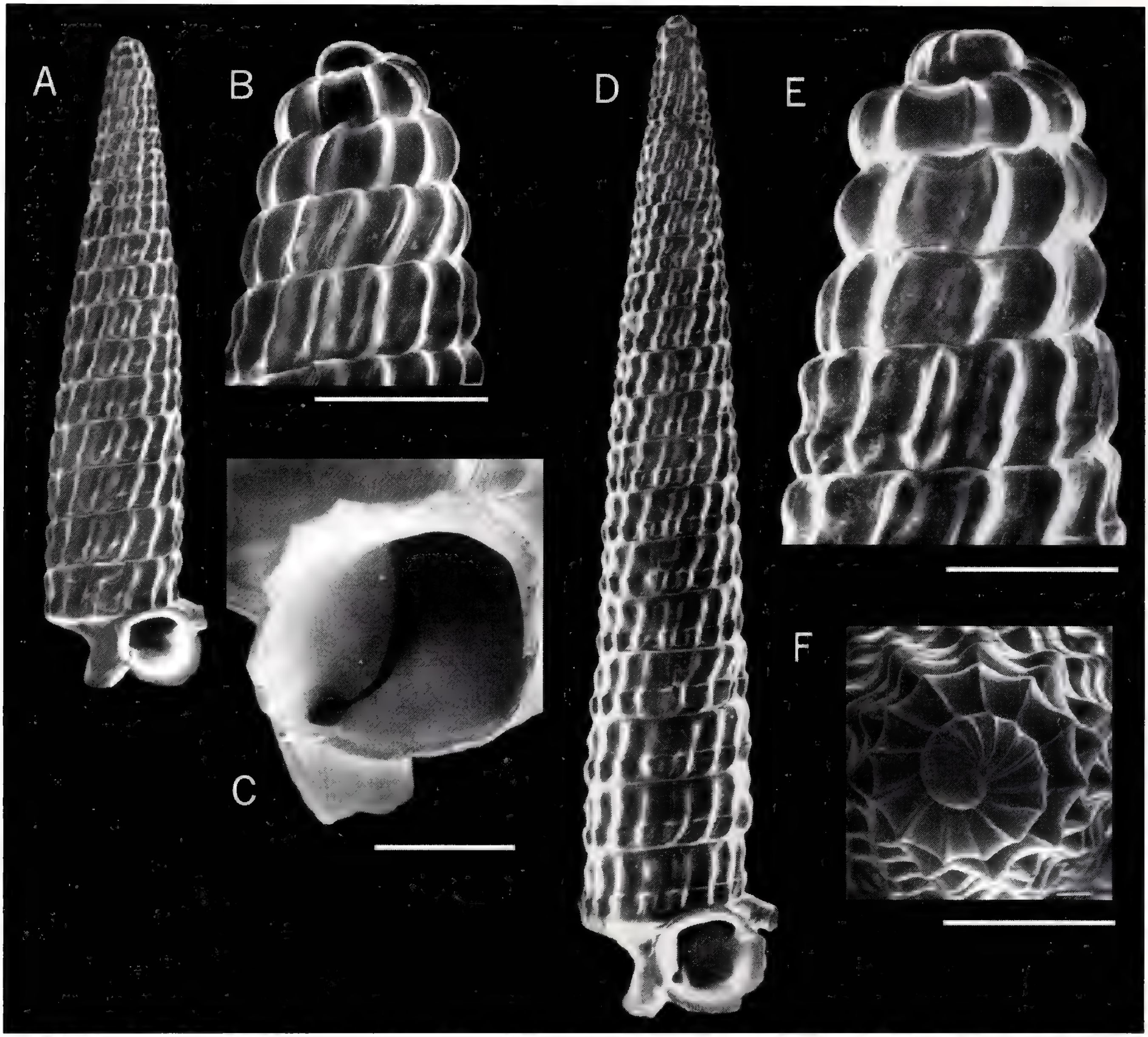

Fig. 8. *Trituba fallax* n. sp. **A.** Holotype from Hyères bank, DW 188 (8.8 mm long). **B.** Protoconch of the holotype. **C.** Oblique view of the aperture of the holotype, to show the closely set edges of siphonal canal. **D.** Specimen from Irving bank, DW205 (15.2 mm long). **E.** Protoconch, same specimen as D. **F.** Apical view of protoconch of another specimen from Irving. Scale bars = 500 μm.

teleoconch. However, it grew much larger (maximum length usually over 10 mm) and had more whorls than *T. anelpistos*. The protoconch was accordingly broader and had more widely spaced ribs, particularly on the first whorl. The siphonal and the anal canals were much shorter, even in the small specimens, and the ribs on the teleoconch formed more distinct bulges. *Trituba constricta* was commonly of similar size but the protoconch had a delicate sculpture, the body whorl was constricted, and the axial ribs, if well developed, had more distinct bulges.

The description above is based on specimens from Hyères, but there were specimens collected on Irving bank tentatively assigned to *Trituba fallax*. The largest one (Fig. 8, D-E) had 23 whorls and resembled *Trituba elatissima* from Plato bank. However, the protoconch sculpture is stronger and the shell surface is glossy (even fresh shells of *T. elatissima* are dull). In addition, the teleoconch sculpture forms ribs similar to those of the pyramidellid genus *Turbonilla* Risso, 1826 in *T. fallax*, whereas in *T. elatissima* the nodose pattern is prevalent.

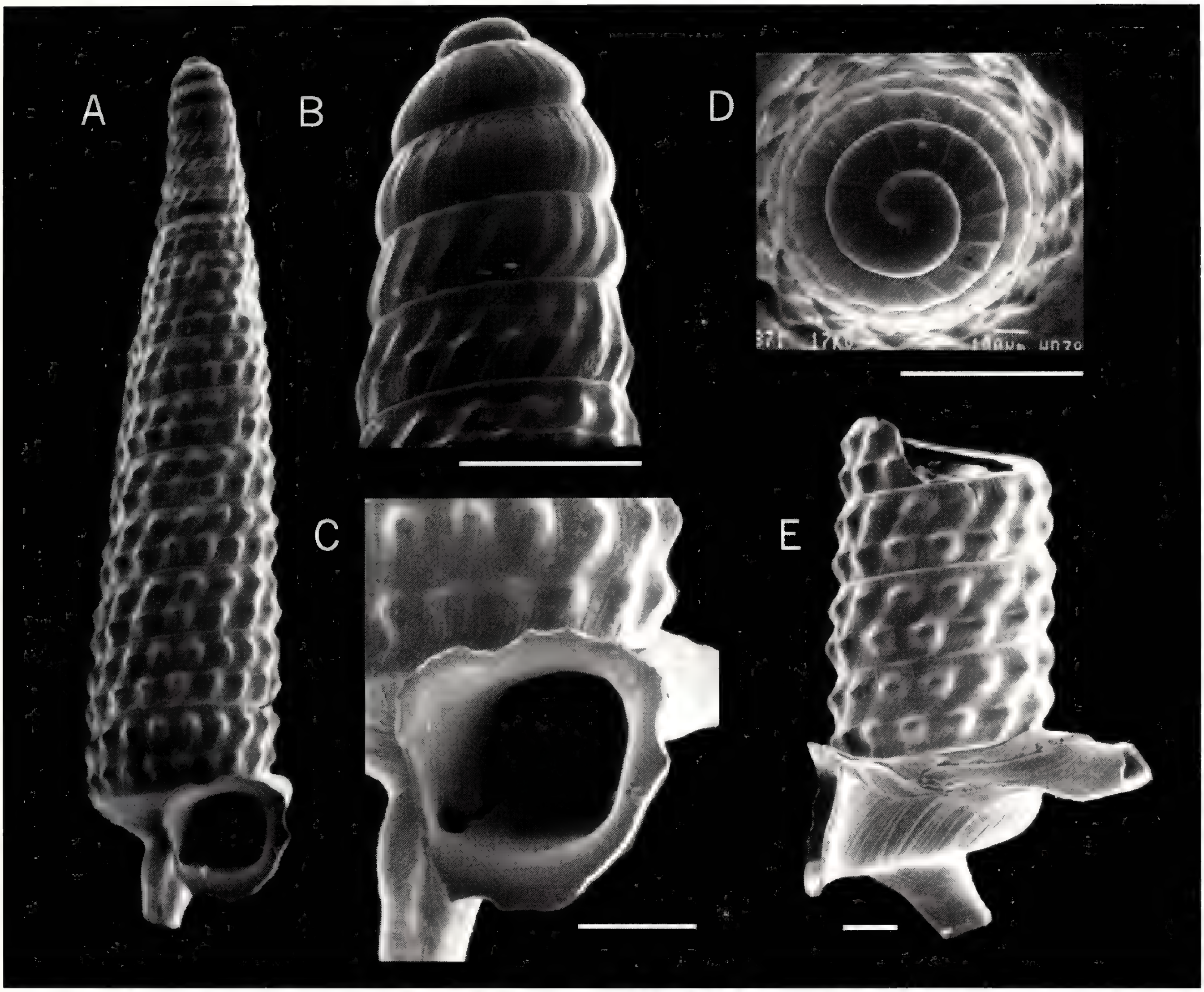

Fig. 9. *Trituba recurvata* n. sp. **A.** Holotype from Hyères bank, DW 203 (8.5 mm long). **B.** Protoconch of the holotype. **C.** Oblique view of the aperture of the holotype, to show the inside of siphonal canal (external tubes are incompletely shown). **D.** Apical view of the protoconch of another specimen. **E.** Lateral view of another specimen, to show the long, curved anal canal. Scale bars = 500 µm.

Trituba recurvata Gofas, new species
(Fig. 9)

Type material

Holotype: (spm., 8.5 x 1.9 mm) and paratypes, 3 spm (adult, 12.3 x 2.3 mm, other 2 with broken apex) and 15 sh. (10 adult, 7.3 x 1.8 to 13.2 x 2.5 mm) from Seamount 2 sta. DW203.

Type locality

Hyères bank, 31°09.5'N - 28°43.5'W, 845m.

Other material examined

Hyères bank, DW184: 3 sh. (9.6 x 2.3 mm, others broken); DW200: 2 spm. (1 adult, 10.8 x 2.0 mm) and 22 sh. (7 adult, 5.5 x 1.5 to 11.5 x 2.3 mm); DW202: 1 sh. (8.1 x 1.9 mm).

Description

Shell up to 13.2 x 2.5 mm, turriculate, solid, white, with 15-20 whorls. Protoconch ca. 3-31/2 whorls, the nucleus moderately protruding, with a somewhat pupoid profile, inflated so as to depart slightly from the general spire profile; protoconch whorls moderately convex, less so along the subsutural portion, sculptured with delicate, irregular, oblique, and flexuous ribs.

Teleoconch whorls sculptured with strong subsutural and suprasutural knobs, arranged in two spiral rows

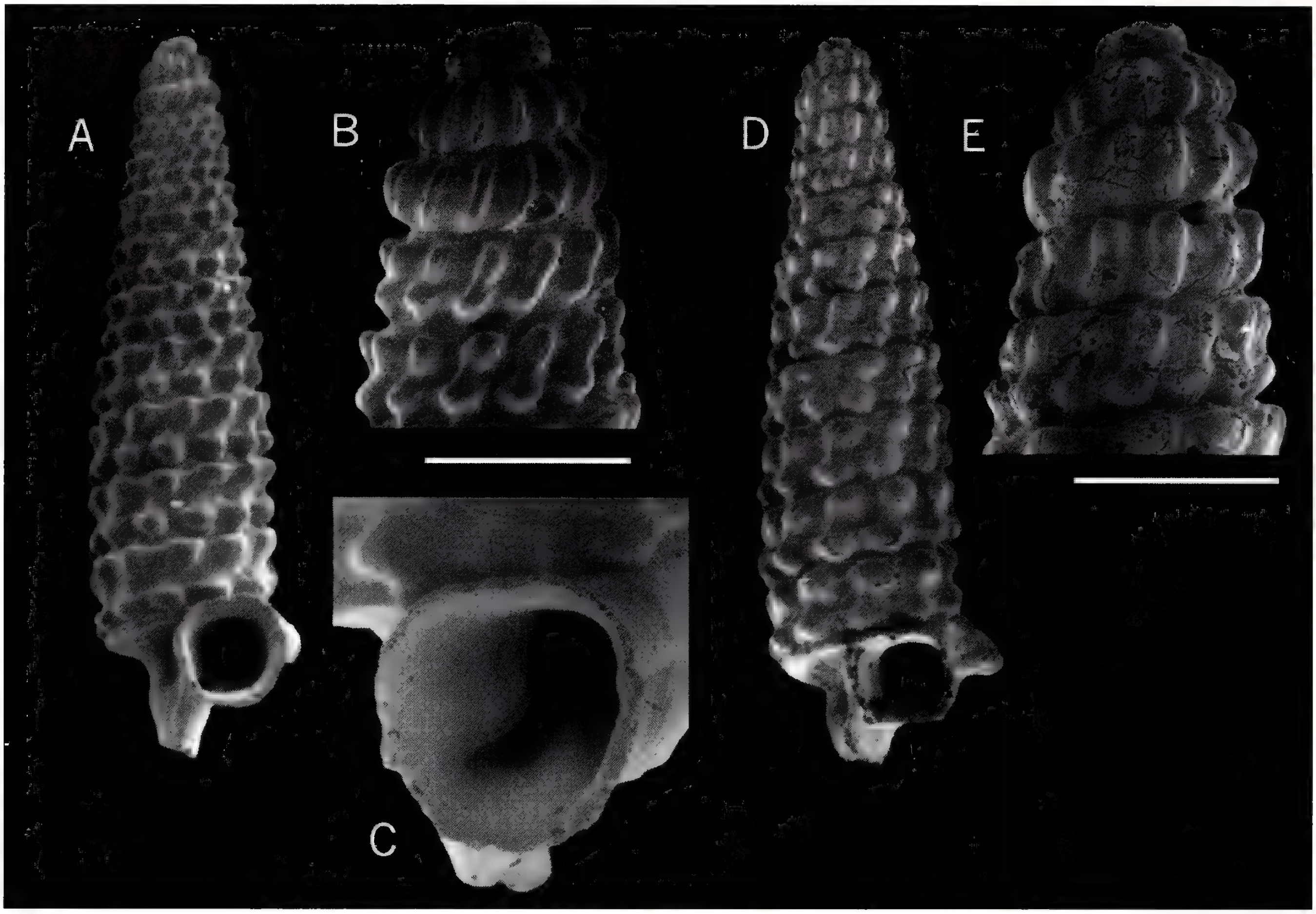

Fig. 10. *Trituba additicia* n. sp. **A.** Holotype from Hyères bank, DW 188 (4.0 mm long). **B.** Protoconch of the holotype. **C.** Oblique view of the aperture of the holotype, to show the widely separated edges of siphonal canal. **D.** Specimen from Irving bank, DW215 (4.2 mm long). **E.** Protoconch, same specimen as D. Scale bars = 500 µm.

which are offset from each other so as to form loosely defined, oblique axial ribs; the suprasutural knobs starting earlier on the first teleoconch whorl and bordered adapically by a definite spiral line. Body whorl hardly narrowing; with the spiral rows of knobs becoming gradually fused and then disappearing; abapical surface smooth and circled by a faint keel.

Aperture with a continuous, flaring peristome. Siphonal canal moderately long, slightly narrowing towards its opening, inside with columellar and labial edges quite close together. Anal canal very long and curved backwards, making a wide angle with apertural plane.

Etymology

The name alludes to the long, curved anal canal.

Remarks

The most similar species was *Trituba incredita* from Meteor bank which differed essentially in having a rather short anal canal. The delicate protoconch sculpture was also found in the sympatric *T. constricta* n. sp., which differed in its larger size, smoother teleoconch sculpture and more predominantly axial, narrowing body whorl and very short canals.

This species was found rather deeper (640-845 m) than the other species on Hyères.

Trituba additicia Gofas, new species
(Fig. 10)

Type material

Holotype (sh., 4.0 x 1.1 mm) from Seamount 2 sta. DW188; Paratypes, 2 sh. (3.6 x 1 mm, 3.2 x 0.95 mm) from Seamount 2 sta. DW182.

Type locality

Hyères bank, 31°30.0'N - 28°59.5'W, 310 m.

Other material examined

Irving bank, DW215: 1 sh. (4.2 x 1.15 mm).

Description

Shell up to 4 x 1.1 mm, turriculate, solid, white, with 10-13 whorls. Protoconch of nearly 3 whorls, with the nucleus quite protruding and the whorls regularly increasing in diameter; protoconch whorls very convex, sculptured with strong, thick ribs, almost axial on the first and second whorl, more oblique on the third whorl (maximum diameter of protoconch 0.6 mm).

Teleoconch whorls sculptured with strong subsutural and suprasutural knobs, arranged in two spiral rows which are offset from each other and connected by faint oblique ridges; both series of knobs starting simultaneously on the first teleoconch whorl, the subsutural one prominent so as to form a channelled suture. Body whorl hardly narrowing; with the abapical surface smooth and circled by a sharp, slightly undulated keel; the subsutural row of knobs abutting against the anal canal, the other one running next to the abapical keel.

Aperture with a continuous, strongly flaring peristome. Siphonal canal moderately long, narrowing towards outer opening, inside with columellar and labial edges quite far apart. Anal canal similar in size and shape to the siphonal, moderately curved backwards.

Etymology

The names means additional, as this species appeared in later sorting of the Seamount 2 material.

Remarks

The sculpture in this species was very strong and resembled that of *Trituba aspera* from Atlantis bank, but the canals were much longer and the protoconch had one more whorl.

Trituba lima Gofas, new species

(Fig. 11)

Type material

Holotype (spm., 9.6 x 2.5 mm, apex broken) and paratypes,

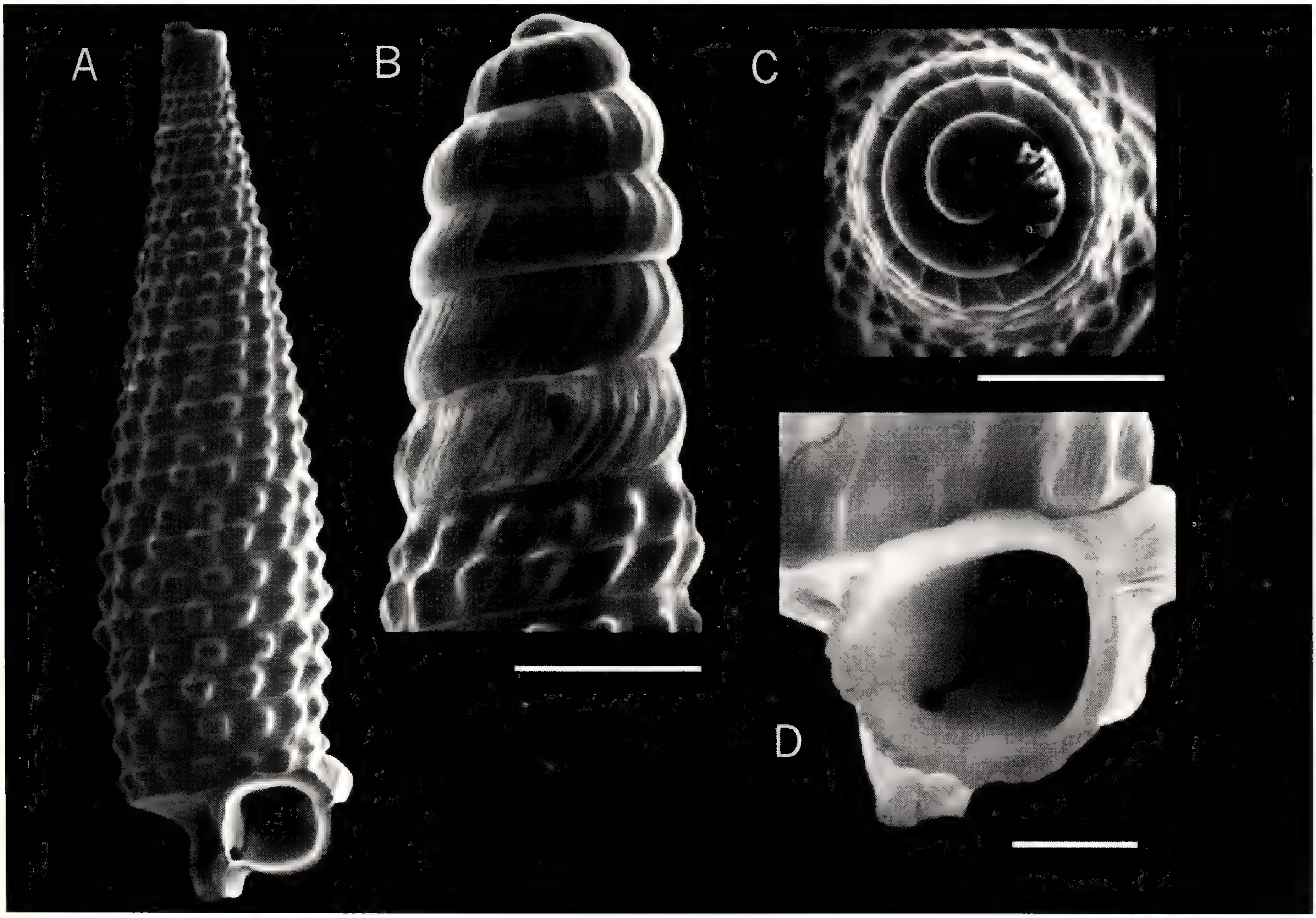

Fig. 11. *Trituba lima* n. sp. **A.** Holotype from Irving bank, DW 237 (9.6 mm long). **B.** Protoconch of another specimen from DW237. **C.** Apical view of the protoconch of another specimen. **D.** Oblique view of the aperture of the holotype, to show the closely set edges of siphonal canal. Scale bars = 500 µm.

7 sh. (3 adult, 8.6 x 2.4 mm, 9.4 x 2.6 mm, 12.5 x 2.9 mm) from Seamount 2 sta. DW237.

Type locality

Irving bank, 32°15.9'N - 27°31.8'W, 670m.

Other material examined

Irving bank, DW225, 4 sh. (3 adult, largest 16.0 x 3.2, broken apex), DW237, 37 sh. (3 adults, broken); DW238: 1 spm. (juvenile) and 11 sh. (3 adult, 9.8 x 2.4 to 13.0 x 3.1, broken apex).

Description

Shell up to 16 x 3.2 mm, fusiform, solid, white, with 19-22 whorls. Protoconch ca. 4-4.5 whorls, with the nucleus quite protruding and a somewhat pupoid profile; protoconch whorls quite convex, the second and third with the suprasutural portion slightly overhanging the following whorl; sculptured with weak ribs, almost axial on the first whorl, more oblique on the following whorls.

Teleoconch whorls sculptured with strong subsutural and suprasutural knobs, arranged so as to form two spiral rows and loosely defined, oblique axial ribs; the suprasutural knobs starting earlier on the first teleoconch whorl and bordered adapically by a definite spiral line, nearly as conspicuous as the suture. Body whorl quite narrowing, its abapical surface smooth and circled by a faint keel.

Aperture with a continuous, hardly flaring peristome. Siphonal canal very short, narrowing towards outer opening, inside with columellar and labial edges coming very close together. Anal canal small and short, pointing sidewards.

Etymology

Alludes to the rough sculpture, like that of a file.

Remarks

This species shared many character states such as size and shape of canals and the general profile, with *Trituba constricta*, and had the teleoconch sculpture as in *Trituba recurvata*. The protoconch had one more whorl than in *T. constricta*, and was broken on most of the adult specimens collected.

Trituba elatissima Gofas, new species

(Fig. 12)

Type material

Holotype (spm. 17.7 x 2.7 mm) and paratypes, 1 spm. (19.8 x 2.7 mm) and 10 sh. (7 adult, 9.5 x 1.7 to 21.2 x 3.3 mm) from Seamount 2 sta. DW248.

Type locality

Plato bank, 33°13.6'N - 29°32.5'W, 735 m.

Other material examined

Plato bank, DW240: 3 sh. (1 adult, 9.0 x 1.8 mm); DW241: 3 sh. (2 adult, broken); DW242: 35 sh. (4 adult, 6.0 x 1.5 to 12.1 x 2.3 mm); DW247: 2 sh. (broken); DW248: 1 spm. and 28 sh. (broken); Atlantis bank, DW255: 2 sh. (juveniles); DW263: 40 sh. (7 adult, 7.6 x 1.5 to 20.8 x 3.0 mm, the latter with apex and lip broken)

Description

Shell up to 21 x 3 mm, turriculate, solid, white, with 13-25 whorls. Protoconch ca. 4-5 whorls, the nucleus moderately protruding; protoconch whorls quite convex, sculptured with strong, sharp, oblique, and curved ribs.

Teleoconch whorls sculptured with strong subsutural and suprasutural knobs, arranged so as to form two spiral rows and loosely defined, oblique axial ribs; the suprasutural knobs starting earlier on the first teleoconch whorl. Body whorl not narrowing; its abapical surface smooth and circled by a keel.

Aperture with a continuous, flaring peristome. Siphonal canal moderately long, cylindrical, inside with columellar and labial edges not very close. Anal canal small and short, pointing sidewards.

Etymology

The name means extremely slender.

Remarks

This species was the only one collected on Plato bank. Large specimens were among the largest of all the seamount *Trituba*, but the smallest specimen (from DW242) was a mere 9 mm high. All, even the small ones, nevertheless had a protoconch with 4 whorls or more. The few specimens collected on Atlantis bank were not in very good condition, but were tentatively assigned to this species. Small specimens resembled the sympatric *Trituba hirta*, although the tubercles on the teleoconch were not so sharp. The main differences lay in the protoconch, which had at least one more whorl and less sharp ribs, and in the aperture, which was more projected.

Trituba hirta Gofas, new species

(Fig. 13)

Type material

Holotype, (sh., 6.3 x 1.7 mm) from Seamount 2 sta. DW274. Paratypes, 3 sh. (adults, 4.9 x 1.4 mm, 6.1 x 1.6 mm, 6.7 x 1.6 mm) from Seamount 2 sta. DW263.

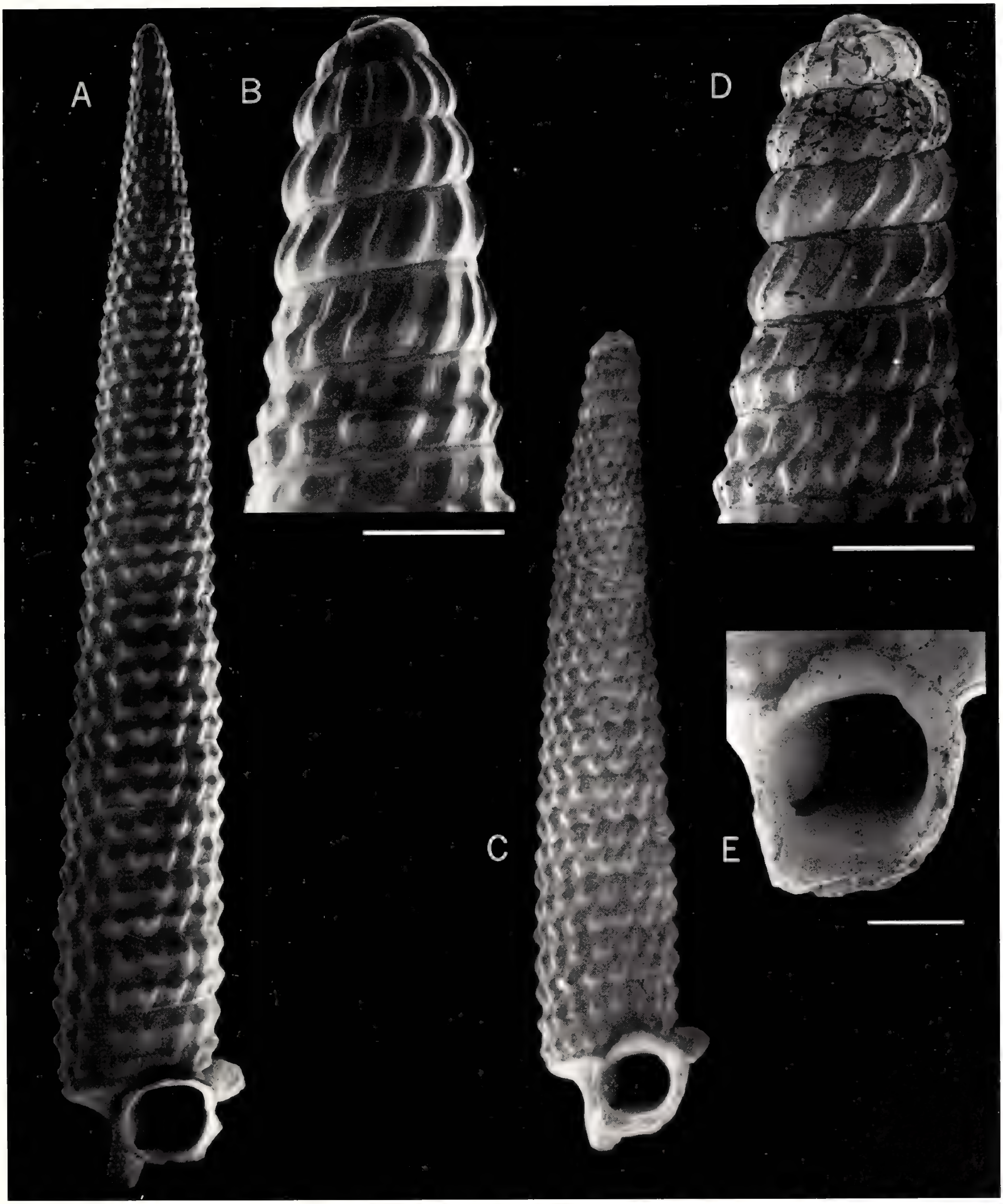

Fig. 12. *Trituba elatissima* n. sp. **A.** Holotype from Plato bank, DW248 (17.7 mm long). **B.** Protoconch of the holotype. **C.** Specimen from Atlantis bank, DW263 (11.7 mm long). **D.** Protoconch, same specimen as C. **E.** Oblique view of the aperture, same specimen as C. Scale bars = 500 μm.

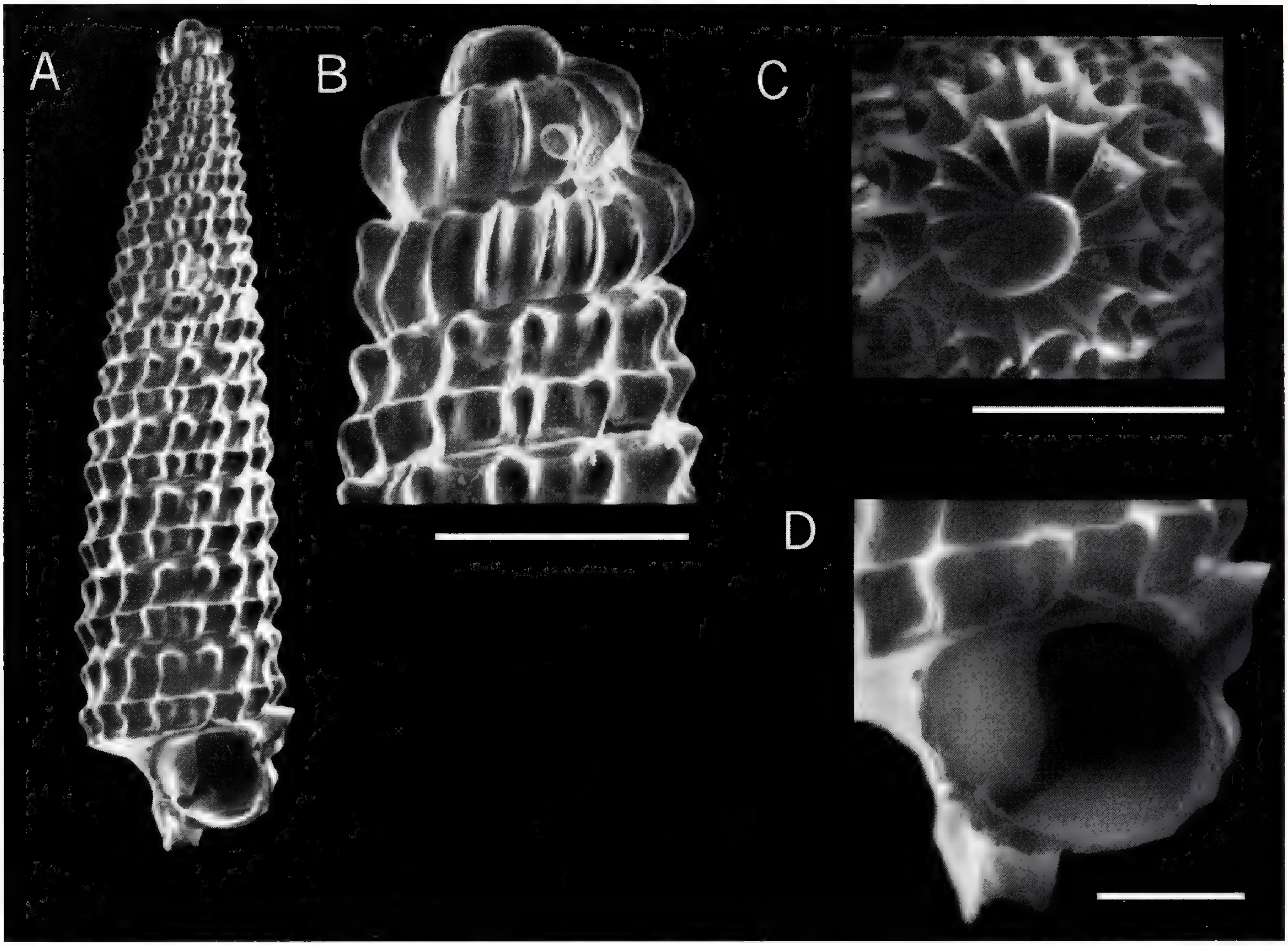

Fig. 13. *Trituba hirta* n. sp. **A.** Holotype from Atlantis bank, DW 274 (6.3 mm long). **B.** Protoconch of the holotype. **C.** Apical view of the protoconch of another specimen from Atlantis bank, DW 255. **D.** Oblique view of the aperture of the holotype. Scale bars = 500 μm.

Type locality

Atlantis bank, 34°05.1'N - 30°13.6'W, 280 m.

Other material examined

Atlantis bank, DW255: 17 sh. (1 adult, 7.2 x 1.7 mm, broken lip); DW258: 5 sh. (1 adult, 7.1 x 1.8 mm).

Description

Shell up to 7.2 x 1.8 mm, turriculate, solid, white, with 14-16 whorls. Protoconch ca. 2-3 whorls, the nucleus moderately protruding; protoconch whorls very convex, sculptured with very strong, sharp, slightly oblique ribs.

Teleoconch whorls sculptured with strong and sharp subsutural and suprasutural knobs, arranged so as to form two spiral rows and loosely defined, oblique axial ribs; both series of knobs starting simultaneously on the first teleoconch whorl, the suprasutural knobs bordered adapically by a definite spiral line. Body whorl not narrowing; its abapical surface smooth and circled by a faint keel on which the axial sculpture abuts.

Aperture with a hardly flaring peristome. Siphonal canal short, slightly narrowing towards its opening, inside with columellar and labial edges moderately close together. Anal canal very short, pointing laterally.

Etymology

The name means hirsute, alluding to the rough protoconch and teleoconch sculpture.

Remarks

Specimens of *Trituba hirta* were rare on Atlantis bank, despite a sampling and sorting effort which was similar to those on Meteor, Hyères, and Irving banks. This species differed from all others described here by its short, very strongly sculptured protoconch and by the rough sculpture of the teleoconch. All specimens examined could be somewhat immature, and it was not clear if both canals would be closed on adult specimens. The fragment of a specimen from the Azores, illustrated by Bouchet and Warén (1993, fig. 1360) was similar for sculpture of both protoconch and teleoconch, but showed one more protoconch whorl and might not be conspecific.

The fossil species *Trituba tertia* (Lozouet, 1999), from the Oligocene of SW France, resembles *Trituba hirta*. It can be distinguished by a smaller protoconch with a more inflated first whorl and a narrow second whorl (see Lozouet, 1999: 58) contrasting with the stout, compact protoconch of the Recent species. However, despite this resemblance, the 25 million year time interval separating these two forms makes it most likely that the resemblance results from convergence in the very few morphological characters involved.

DISCUSSION

Trituba species are now very isolated on the North Atlantic seamounts and the Azores. The only known Recent congeneric species in the Atlantic is *Trituba barbadensis* (Coomans and Faber, 1984), found at 90-100 m depth off Barbados, and morphologically quite different. This Caribbean species has a coarsely ribbed protoconch resembling *Trituba fallax* or *Trituba addititia*, but has a genuine teleoconch sculpture with widely separated suprasutural knobs, which are not found in any of the species treated herein. Additional species are found in the 100-1000 m depth interval of the Indo-Pacific (Marshall, 1977).

The genus is believed to be extinct on the European continental margins, and is not recorded as a fossil in sediments younger than the Miocene. The Late Oligocene fossil representative *Trituba raulini* (Cossmann and Peyrot, 1822) resembles the Recent Atlantic species and may be viewed as a possible ancestor, but is unambiguously distinct at the species level. Material examined from the type locality (Pereyre, Landes, France, collected by P. Lozouet) has a high-conical, multispiral protoconch that is ornamented with delicate ribs and is clearly demarcated from the first teleoconch whorl. This protoconch morphology indicates planktotrophic development and, although equally multispiral, is distinct from the cyrtoconoid profile and gradual protoconch-teleoconch transition seen in the Meteor group species. The same Oligocene locality also yielded *Trituba tertia*, a species believed to have direct development, which has a coarsely ribbed protoconch and is astonishingly similar to the Recent *Trituba hirta* n. sp. I nevertheless have considered it more parsimonious to interpret it as having a convergent morphology, rather than to hypothesize that it has survived 25 million years and colonized the Atlantis bank separately from the other species.

Trituba dujardini (Mayer, 1862) from the Miocene of the shallow epicontinental Touraine basin, France, is quite distinct from both *Trituba raulini* and from the Recent species from the Meteor area in having large, closely set, pearl-like tubercles on the teleoconch, very much in the manner of many littoral Cerithiopsidae. The taxa *Trituba tauroturrita* and *T. tauroturrita* var. *spiraliornata*, described by Sacco (1895) from the Miocene of Northern Italy, also have a coarse sculpture but are based on quite poor material on which not much more can be said.

The ten species recognized here from the Meteor group seamounts show various combinations of a small array of character states, and are best interpreted as the product of a single radiation. However, because all of these shell characters are liable to reversal, the data do not provide evidence for a detailed phylogeny of the species. The occurrence of several discrete and sympatric forms in most sites (3 on Meteor, 5 on Hyères and Irving, 2 on Atlantis; Table 2) supports the view that the morphological differences reflect species-level separation.

The level of bank-to-bank endemism is high. Only

Table 2. Summary of the occurence of *Trituba* species on the Meteor group seamounts. Upper block: species with coarse protoconch sculpture, lower block: species with delicate protoconch sculpture.

Meteor	Hyères	Irving	Plato	Atlantis
superstes				
	additicia	*additicia*		
anelpistos	*anelpistos*	*anelpistos*		
	fallax	*fallax*		
				hirta

incredita				
	recurvata			
	constricta	*cf. constricta*		
		lima		
			elatissima	*cf. elatissima*

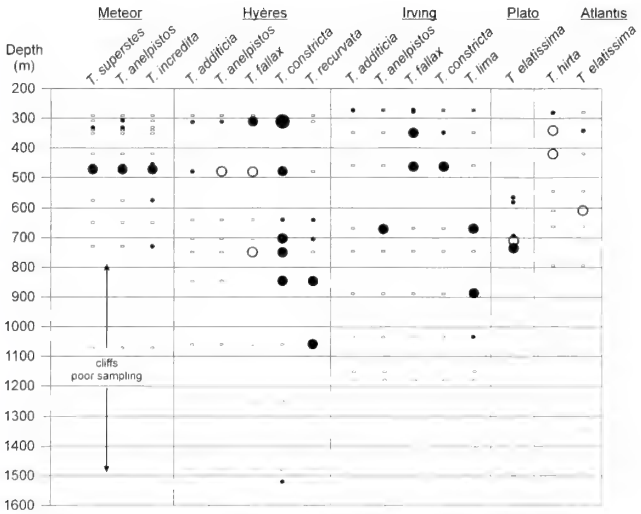

Fig. 14. Plot of the occurrence of *Trituba* species versus bathymetry in the material from Seamount 2 cruise. Dashes: samples without occurrence of *Trituba*; dots: 1-4 shells present; open circles: more than 4 shells, no living specimens; solid circles: living specimens present. Samples below 1600 m did not yield *Trituba* and are not shown.

Trituba anelpistos is found on three banks; four species are found on Hyères and Irving, one is shared between Plato and Atlantis, and the remaining four species are endemic to one bank. With the exception of *Trituba lima*, single-bank endemic species are found on the most external banks, viz. Meteor and Atlantis. Between Hyères and Irving, conversely, four out of five species are shared.

This pattern indicates that the distances between the banks, in the order of 100 to 200 km, are a barrier for larvae and egg capsules of *Trituba*, and that this could account for the speciation events in this species group. The reproductive biology is not known from direct evidence, and there were no egg capsules recorded among the material, despite sorting down to the 0.5 mm fraction. Although there is a multispiral protoconch, the larval development in the Recent North Atlantic species is inferred to be intracapsular from similarity of the larval whorls with those of *Cerithiella* (see Bouchet and Warén, 1993).

The barrier, however, is not absolute. Intracapsular larval development does not preclude dispersal into a broad geographic range (e.g. *Cerithiella metula* [Lovén, 1846]), and the endemic pattern of *Trituba* contrasts with that of most of the other direct developers of the seamounts that are found on more than one bank (e.g. the fasciolarid *Fusinus meteoris* Gofas, 2000; the muricid *Poirieria actinophora* [Dall, 1889], see Houart, 1996). In the case of *Trituba*, there must be an additional cause which would preclude rafting. Brooding can be ruled out because the morphology of the shell does not allow space for it, and a possible scheme would be some kind of nesting or embedding the egg capsules in the sponges on which the animal lives. Another possible explanation would be interspecific competition, which could impede successful colonization by one species where another one is well established.

From the above considerations, there is no straightforward conclusion regarding whether *Trituba* has colonized the seamounts as a planktotrophic species similar to *Trituba raulini*, which later lost planktotrophy in local populations, or whether it arrived as a non-planktotrophic species resembling *Trituba tertia*. In any case, the original colonization must predate the extinction on the European margin in the Miocene. The seamounts are older, 50-76 million years for the Irving-Cruiser plateau (Tucholke and Smoot, 1990), and were close to the sea surface at the time of *Trituba raulini* (see Fermont and Troelstra, 1983).

There appears to be great differences in the success of the different species, as reflected by their relative abundances, ranging from the 64 specimens and over 500 shells collected of *Trituba constricta* to the mere 4 shells of *Trituba additicia*. Some of the rarer species (e.g. *Trituba additicia, Trituba hirta, Trituba constricta*) could be very prone to extinction or may even be extinct. The rate of species turnover generated by successive back and forth colonization compensating extinctions is not known, but the global balance is such that it has allowed the persistence of the genus on the banks despite its extinction along the European mainland. Moreover, the diversification into a set of separate species with distinct bathymetric ranges (Fig. 14) and with different sizes and shapes could result in unequal susceptibility to predators and other extinction risk factors, and thus is likely to greatly enhance the probability of survivorship of the lineage as a whole. *Trituba recurvata* on Hyères and *Trituba lima* in Irving have a deeper bathymetric range (650-1100 m approximately) than the bulk of the species, which are found on the upper portions of the seamounts.

The common species suffer high predation pressure, as evidenced from the incidence of gastropod drillings on the large populations of *Trituba constricta* (one third to two thirds of the adult shells drilled in the large lots). The elongated shape, which allows the animal to withdraw deep into its shell, and the complicated aperture appear to provide good protection against crab predation (only seen with high impact on Atlantis bank). The heavier sculpture should be a protection against drilling but does not seem effective. The species responsible for drilling is probably the muricid *Poirieria actinophora*. There are no clues to how much time the drilling gastropods have been around, but they may be a relatively new element of the fauna since there is no detectable morphological difference between seamount and Caribbean specimens (which also rely on unpredictable rafting for dispersal). Thus, it is not certain that the current morphology in *Trituba* represents the best adaptive response to this predator.

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Cephalaspidea *s. l.* (Mollusca: Opisthobranchia) of the Madeira Archipelago and Selvagens Islands, northeast Atlantic, Portugal*

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Abstract: A total of 37 species of cephalaspidean opisthobranchs have been recorded in the literature from the Madeira Archipelago and the Selvagens Islands. More than half of these records date from the 19th century. In this paper, two new records are added: *Chelidonura africana* Pruvot-Fol, 1953 and *Chelidonura sabadiega* Ortea, Moro and Espinosa, 1996; the latter recently described from El Hierro, Canary Islands. Anatomical data on *Bulla mabillei* are provided. The radula of this species and those of *Ringicula conformis, Haminoea hydatis* and *Haminoea orteai* are illustrated using scanning electron microscopy. Morphological details of the shells of six species (*Ringicula conformis, Bulla mabillei, Philine catena, Retusa truncatula, Retusa mammillata,* and *Retusa* sp.) are also described. The presence of *Haminoea orteai* (previously recorded twice from the eastern Atlantic, both as *Haminaea* cf. *orteai*) allows us to expand the range of this species.

The faunistic affinities of the cephalaspideans from Madeira are studied by cluster analysis. This analysis shows a high affinity between Madeira and the Canary Islands, within a group formed by Mauritania, Senegal, and Cape Verde, and suggests the existence of a "boundary" between the Azores and Madeira that makes those archipelagoes more similar to the Lusitanian and Mediterranean regions, respectively, than to each other.

Key Words: Opisthobranchia, Cephalaspidea, Madeira, Selvagens, Taxonomy

Previous knowledge on cephalaspidean opisthobranchs from the Madeira archipelago and the Selvagens Islands is restricted to isolated references to several species, found in general monographs on molluscs. Systematic and biogeographic data on the cephalaspideans from this geographic area are not available. Most previous records were based on empty shells, from expedition dredges, or by individual collectors in Madeira and Porto Santo Islands, and there are several species whose identities are doubtful. A total of 37 species of cephalaspideans have been recorded in this area, in 16 published works: McAndrew (1852), Watson (1878; 1886; 1891; 1897), Nobre (1889; 1894; 1895; 1937), Locard (1897), Nordsieck (1972), Talavera (1978), Nordsieck and García-Talavera (1979), Wirtz (1995), Malaquias and Calado (1997), and Malaquias (2000).

Among the opisthobranchs, cephalaspidean molluscs have been traditionally considered as a transitional group situated between the "prosobranchs" and the higher opisthobranchs. As Mikkelsen (1993: 118) pointed out, the taxonomic history of this group has been "one of repeated inclusions and exclusions, expansions and restrictions." Several taxonomic rearrangements have been made on this group in light of new data and new techniques for analysis. For instance Haszprunar (1985) and Salvini-Plawen (1988; 1991a, b) proposed the exclusion of six families from the Cephalaspidea. More recently Mikkelsen (1996) removed *Ringicula, Hydatina*, and *Acteon* from the traditional cephalaspideans, whereas the remaining groups constituted the Cephalaspidea *sensu stricto*.

In April 1994, the Museu Municipal do Funchal (História Natural) began a research program on opisthobranch molluscs in the archipelago of Madeira and the Selvagens Islands called *OpisthoMadeira*. The objective of this paper is to present the results on the cephalaspidean opisthobranchs recorded during that program.

METHODS

The Archipelago of Madeira lies in the Atlantic Ocean between parallels 33°07'N and 32°24'N and meridians 16°17’W and 17°16’W (Fig. 1). It consists of the islands of Madeira, Porto Santo, and the three Desertas as well as some small islets around these main islands. The Selvagens Islands (Selvagem Grande, Selvagem Pequena, and Ilhéu de Fora), located 160 miles South of Madeira (30°09’N - 30°01’N and 15°56’W - 16°03’W), also belong to the Madeira Archipelago (Portugal).

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*Contribution of the Instituto Português de Malacologia

According to the biogeographic areas defined by Ekman (1953) and Briggs (1974), the Archipelago of Madeira and the Selvagens Islands belong to the Mauretanian region. However, these islands together with the Canary Islands, Azores, and Cape Verde, are often included in the Macaronesian biogeographical region (Mitchell-Thomé, 1976; Beyhl *et al.*, 1995; Sjögren, 2000).

Material was collected from the Selvagens between July and August 1994 and in April 1996. Samples were obtained by SCUBA diving, using a suction device to survey the upper layers of sediments at depths between 10-25 m. Six stations were established on Selvagem Grande.

Madeira was sampled between 1994 and 1998, primarily at six locations (Fig. 1; Table 1). Several sampling methods were used, including manual collection, use of a suction device during SCUBA diving, and removal of organisms by brushing subtidal rocks. At Garajau, a Van Veen grab was used to obtain samples along a transect in depths of 20, 25, 50, 75 and 100 m.

After sieving, the specimens were preserved in 70% ethanol and deposited in the collections of the Museu Municipal do Funchal (História Natural), abbreviated MMF(HN). Radulae were obtained by dissolving the buccal mass in a solution of 10% sodium hydroxide, warmed on a hot plate. Radulae were rinsed, dried, mounted, and coated with gold for SEM.

The faunistic affinities of the Madeiran and Selvagens cephalaspideans were investigated using the variability of all species present in the following geographic areas: British Isles, Lusitania (French, Spanish and Portuguese Atlantic coasts), Azores, Canary Islands, Cape Verde, Mauritania (from Ceuta to the Capo Blanco coasts), Senegal, and the Mediterranean Sea. The Jaccard similarity index was used (Krebs, 1989). The results were graphed as a dendogram, using the UPGMA aggregation algorithm (Sneath and Sokal, 1973). Calculations were performed with the software package NTSYS-pc 2.02c (Numerical Taxonomy and Multivariate Analysis System). Species checklists were compiled by combining the information obtained from the authors and from the following bibliographic sources: British Isles (Thompson, 1988), Lusitania (Cervera *et al.*, 1988; Thompson, 1988), Azores (Mikkelsen, 1995), Canary Islands (Cervera *et al.*, 1988; Ortea *et al.*, 1996; Ortea and Moro, 1998), Cape Verde (Cosel, 1982a, b; Ortea *et al.*, 1990, Linden, 1995; Ortea and Moro, 1998), Mauritania (Dautzenberg, 1910; Nicklès, 1950; Pasteur-Humbert, 1962; Bellon-Humbert, 1974); Senegal (Dautzenberg, 1910; Fischer-Piette, 1942; Braga, 1947; Nicklès, 1950) and Mediterranean Sea (Cervera *et al.*, 1988; Cattaneo-Vietti and Thompson, 1989).

Table 1. Geographical coordinates of the sampling localities.

Number of the sampling localities	Geographical coordinates
1	32° 38’ 00”N - 16° 55’ 51”W
2	32° 38’ 23”N - 16° 52’ 19”W
3	32° 38’ 46”N - 16° 53’ 46”W
4	32° 43’ 54”N - 16° 43’ 53”W
5	32° 44’ 14”N - 16° 42’ 54”W
6	32° 46’ 11”N - 16° 49’ 21”W
7	30° 08’ 19”N - 15° 52’ 20”W
8	30° 08’ 17”N - 15° 52’ 11”W
9	30° 08’ 16”N - 15° 52’ 00”W
10	30° 08’ 08”N - 15° 51’ 43”W
11	30° 08’ 09”N - 15° 51’ 29”W
12	30° 08’ 09”N - 15° 51’ 16”W

RESULTS

There are 38 species of cephalaspideans known from Madeira and the Selvagens Islands, 37 previously cited in the literature - one of them *Runcina adriatica* is here considered as a misidentification (see comments below) - and two are added in this study. In most cases the identities of these species were established on the basis of the shell morphology only, whereas the soft parts remained undescribed.

From the samples collected during the project *OpisthoMadeira* a total of 14 species were found, all of them in shallow waters, with a maximum depth of 100 m. For each species the number of specimens studied is given, and whether they were complete specimens or empty shells. Comments on the taxonomic identity and details of the internal anatomy are given for some species. Asterisks indicate that specimens were collected alive.

Order CEPHALASPIDEA *s. l.*
“ARCHITECTIBRANCHIA or LOWER HETEROBRANCHIA”
(according to Mikkelsen [1996: 422])

Family ACTEONIDAE D’Orbigny, 1842

Japonacteon? pusillus (Forbes, 1843)
Previous records: Watson (1886: 627; 1897: 272); Nobre (1937: 13); Nordsieck and García-Talavera (1979: 169), all as *Acteon pusillus*; Nordsieck (1972: 8, as *Pseudactaeon*

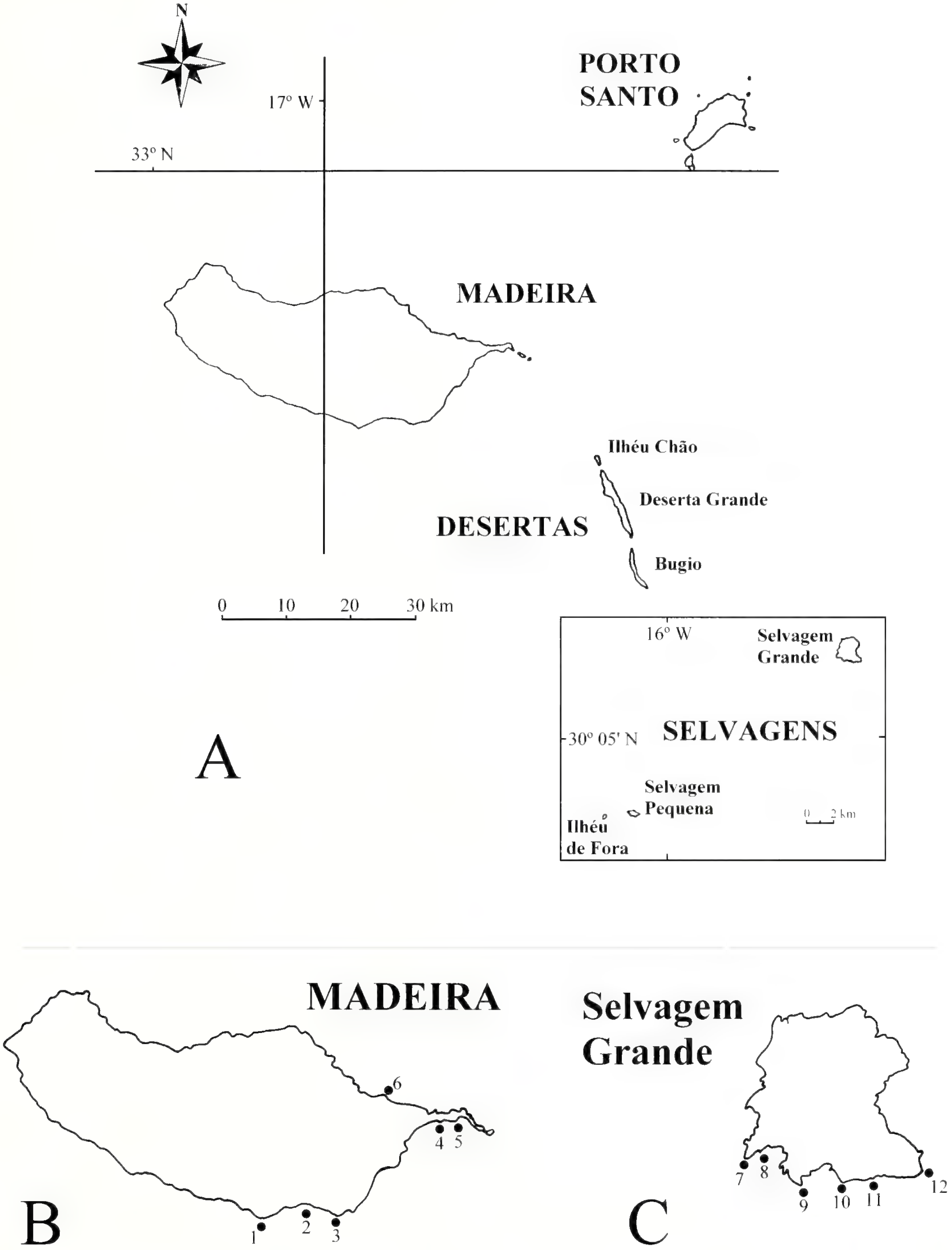

N
17° W
33° N
PORTO
SANTO
MADEIRA
Ilhéu Chão
Deserta Grande
DESERTAS
Bugio
0
10
20
30 km
16° W
Selvagem
Grande
30° 05' N
SELVAGENS
Selvagem
Pequena
Ilhéu
de Fora
0
2 km
A
MADEIRA
6
4
5
1
2
3
B
Selvagem
Grande
7
8
9
10
11
12
C

Fig. 1. A. Map of the Madeira Archipelago and the Selvagens Islands. B. Sampling localities in Madeira Island: 1, Lido of Funchal; 2, Lazareto; 3, Garajau; 4, Junta do Caniçal Harbor; 5, Quinta do Lorde; 6, Porto da Cruz. C. Sampling localities in Selvagem Grande Island: 7, Ponta da Atalaia; 8, Enseada das Cagarras; 9, Restinga; 10, Ponta do Inferno; 11, Fonte Salgada; 12, Ponta do Leste.

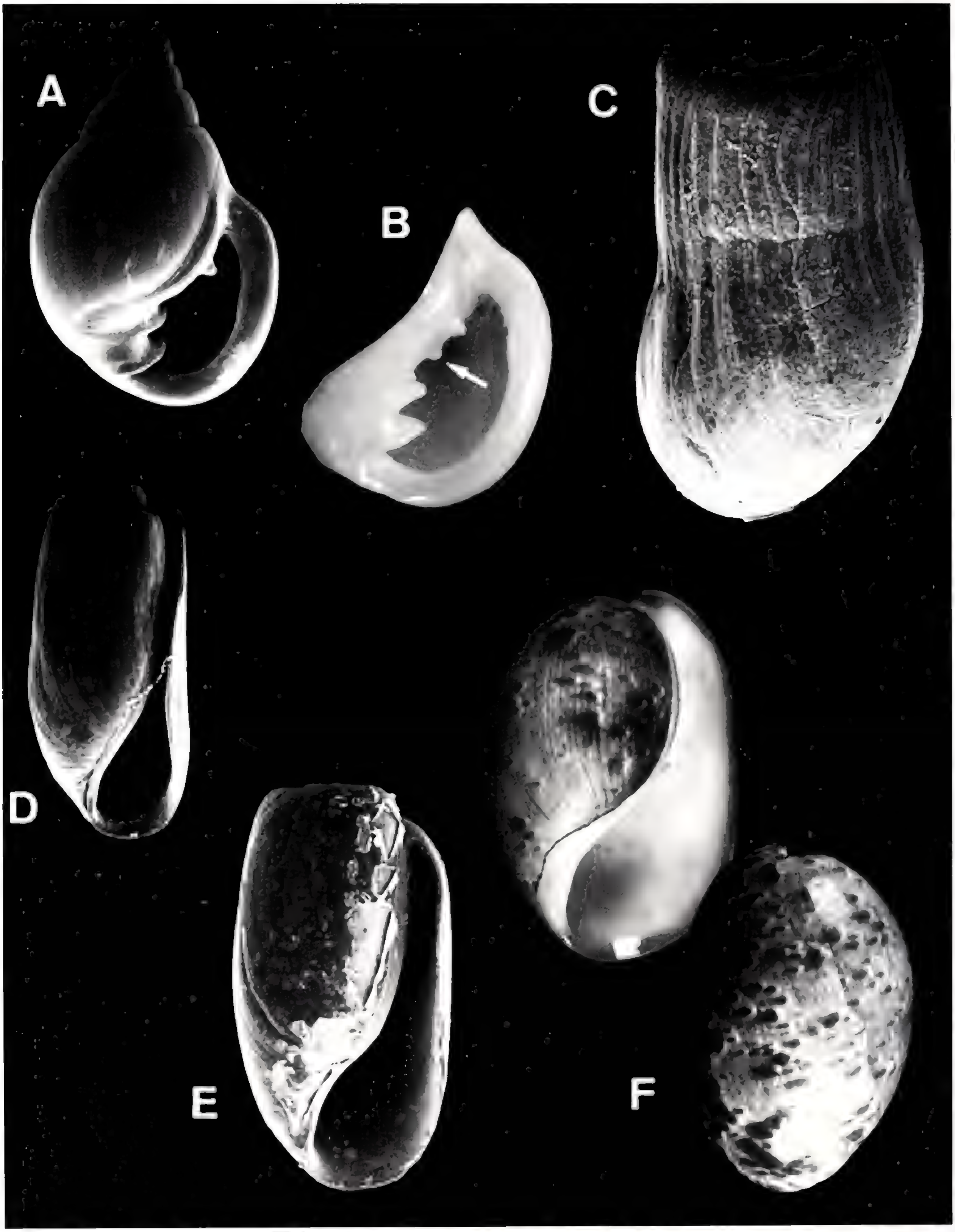


Fig. 2. Shells of selected species. A. *Ringicula conformis*, thick-lipped specimen, 3.2 mm long. B. Detail of the same specimen, showing the innermost parietal tooth. C. *Retusa truncatula*, 1.5 mm long. D. *Retusa mammillata*, 3.6 mm long. E. *Retusa* sp., 1.6 mm long. F. *Bulla mabillei*, 47 mm long.

pusillus), Madeira Island.
Remarks: Not collected in the present study.

Colostracon amabile (Watson, 1883)
Previous records: Nordsieck (1972: 10); Nordsieck and García-Talavera (1979: 169), as *Colostracon (Ovactaeonina) amabilis*, Madeira Island.
Remarks: Not collected in the present study.

Acteon tornatilis (Linné, 1767)
Previous records: Watson (1897: 272); Nobre (1937: 13); Nordsieck and García-Talavera (1979: 168), Madeira Island.
Remarks: Not collected in the present study.

Family RINGICULIDAE Meek, 1862
Ringicula auriculata (Ménard, 1811)
Previous records: McAndrew (1852: 107); Watson (1897: 307); Nobre (1937: 16); Nordsieck (1972: 11); Nordsieck and García-Talavera (1979: 169), Madeira, ?Porto Santo Islands.
Remarks: Not collected in the present study.

Ringicula conformis Monterosato, 1877* (Figs. 2A-B, 3A)
Previous records: Nobre (1889:16); Nordsieck and García-Talavera (1979: 170 as *Ringicula [Plicatra] conformis*), Madeira.
Remarks: There are no references for the Selvagens Islands.
Material examined: Madeira, Garajau, 20-100 m depth, 106 empty shells (MMF[HN] 30691/30694/30695/30697/30698/30699/30700); Lido, 20 m depth, one living specimen (shell 3.1 mm long), (MMF[HN] 31001).
Description: The shell is white and globose with smooth surface; the spire is conical, typical in the genus. There are two well-developed folds on the columella ("columellar teeth"), and two small teeth ("parietal teeth") posteriorly, on the inner lip (Figs. 2A-B). Both inner and outer lips may be thick and heavily callouse. This variability agrees with that found by Ciccone and Savona (1982: 26) in the Mediterranean Sea. These authors described four teeth within the inner lip. All the examined specimens from Madeira have smooth surfaces; although it seems that in some localities individuals have some vertical folds on the posterior whorls (Pilsbry, 1895: 396). The radular formula is 24 x 1-0-1, the lateral tooth smooth, claw-shaped (Fig. 3A).
Remarks: *Ringicula* is one of the lesser known genera of the traditional Cephalaspidea, most of the species being described only on the basis of the shell. Pelseneer (1924) studied the anatomy of *R. conformis*, and gave the radular formula 1-0-1. Gosliner (1994: 279) pointed out that in all the examined species of *Ringicula*, the radula "consists of a single row of lateral teeth on either side of the rachis, which lacks a rachidian row." Both the radular formula and the shape of the lateral tooth are generic (not specific) characters.

Ringicula someri De Folin, 1867
Previous records: Nobre (1889: 16; 1894: 144; 1937: 17); Watson (1897: 307); Nordsieck and García-Talavera (1979: 169), Madeira Island.
Remarks: Not collected in the present study.

Family APLUSTRIDAE Gray, 1847

Hydatina physis (Linné, 1758)
Previous records: Wirtz (1995: 185).
Remarks: Wirtz (1995) illustrated a specimen from the Canary Islands. The reference to Madeira is made on the basis of a shell present at the collections of the MMF(HN). Not collected in the present study.

CEPHALASPIDEA *s.s.* (according to Mikkelsen [1996: 422])
Family DIAPHANIDAE Odhner, 1914

Diaphana minuta (Brown, 1827)
Previous records: McAndrew (1852: 108, as *Amphisphyra hyalina*). Nordsieck and García-Talavera (1979: 173, as *Micromelo minuta*), Madeira, ?Porto Santo Islands.
Remarks: Not collected in the present study.

Diaphana flava (Watson, 1897)
Previous records: Watson (1897: 234, as *Amphisphyra flava*); Nobre (1937: 18, as *Amphisphyra flava*); Nordsieck and García-Talavera (1979: 173, as *Micromelo flava*), Madeira Island.
Remarks: Not collected in the present study.

Family RETUSIDAE Thiele, 1926

Retusa truncatula (Bruguière, 1792)* (Fig. 2C)
Previous records: Watson (1897: 326 as *Utriculus truncatulus*); Nobre (1937: 14 as *Tornatina truncatula*); Nordsieck and García-Talavera (1979: 176 as *Retusa mariae*), Madeira. Nobre (1937: 14 as *Tornatina truncatula*); Nordsieck (1972: 34, as *Retusa mariae*), Porto Santo Island. Malaquias and Calado (1997: 153), Selvagens Islands.
Material examined: Selvagem Grande, Ponta do Inferno, one empty shell (1.06 mm long) (MMF[HN] 30703); Enseada das Cagarras, one empty shell (1.5 mm long). Both found at 15-16 m depth.
Remarks: Only empty shells were collected. Identification is thus based on shell morphology, which is cylindrical, slightly expanded anteriorly, with a flat spire and a visible protoconch. As Mikkelsen (1995: 206) described for

Azorean specimens, the sculpture of the white shell is "smooth anteriorly, and with strong axial ribs posteriorly." (Fig. 2C).

Cylichnina umbilicata (Montagu, 1803)
Previous records: Watson (1897: 284, as *Cylichna umbilicata*); Nobre (1937: 13, as *Tornatina umbilicata*); Nordsieck and García-Talavera (1979: 177, as *Cylichnina subcylindrica*), Madeira Island.
Remarks: Not collected in the present study.

Retusa leptoeneilema (Brusina, 1865)
Previous records: Talavera (1978: 126); Nordsieck and García-Talavera (1979: 176, as *R. leptoleynema*); Malaquias and Calado (1997: 153), Porto Santo and Selvagens Islands.
Remarks: Not collected in the present study.

Retusa mammillata (Philippi, 1836) (Fig. 2D)
Previous records: Nordsieck (1972: 36 as *Mamilloretusa mamillata*). Porto Santo: Nordsieck and García-Talavera (1979: 176 as *M. mamillata*), Madeira. Talavera (1978: 126); Nordsieck and García-Talavera (1979: 177 as *M. mamillata*); Malaquias and Calado (1997: 153), Selvagens Islands.
Material examined: Selvagem Grande: Ponta da Atalaia, at 16 m, one empty shell (3.7 mm long) (MMF[HN] 30704).
Remarks: The shell is smooth, with an elevated first whorl or protoconch (Fig. 2D). Lemche (1948: 55) suggested that *R. mammillata* should be synonymized with *R. truncatula*, which was accepted by several authors, such as Thompson (1976: 113) and Mikkelsen (1995: 207). Nevertheless, Aartsen *et al.* (1984: 46) stated that *R. mammillata* can be distinguished by the protuding apex, the cylindrical contour and, above all, by a sculpture of spirally incised lines instead of the more or less pronounced axial folds of *R. truncatula.*

Retusa tornata (Watson, 1883)
Previous records: Watson (1886; 1897: 326, as *Utriculus tornatus*); Nobre (1937: 14, as *Utriculus tornatus*); Nordsieck (1972: 36, as *Semiretusa tornata*); Nordsieck and García-Talavera (1979: 177, as *S. tornata*), Madeira and Porto Santo Island.
Remarks: Not collected in the present study.

Retusa sp.* (Fig. 2E)
Material examined: Selvagem Grande, Ponta da Atalaia, two specimens (MMF[HN] 30685) and three empty shells (1.4-1.6 mm long), found at shallow depth.
Remarks: One dissected specimen lacks radula and jaws, whereas the three uncalcified gizzard plates are tuberculate. We were unable to attribute these specimens to any of the known species of *Retusa* based on shell morphology (Fig. 2E), although their small size suggests they could be young specimens of *R. mammillata.*

Cylichnina nitidula (Lovén, 1846)
Previous records: Locard (1897: 68); Watson (1897: 326 as *Utriculus nitidulus*); Nobre (1937: 14 as *Utriculus nitidulus*); Talavera (1978: 126, as *Retusa nitidula*); Nordsieck and García-Talavera (1979: 177), Madeira and Porto Santo Islands.
Remarks: Not collected in the present study.

Family CYLICHNIDAE Rudman, 1978

Cylichna cylindracea (Pennant, 1777)
Previous records: McAndrew (1852: 108); Nobre (1895: 97); Watson (1897: 284); Nobre (1937: 15), Madeira. Locard (1897: 68). Porto Santo: Nordsieck (1972: 15); Nordsieck and García-Talavera (1979: 170), Desertas Islands. There are no references for the Selvagens Islands.
Material examined: Madeira, Garajau, 20-100 m depth, 11 empty shells (2.4-5.1 mm), (MMF[HN] 30689/30696/30702).
Remarks: No living specimens of the species were collected. Identification was made on the basis of shell morphology, which is involute and cylindrical.

Pyrunculus spretus (Watson, 1897)
Previous records: Watson (1897: 234 as *Cylichna spreta*); Nobre (1937: 15 as *C. spreta*); Nordsieck and García-Talavera (1979: 170 as *C. spreta*), Madeira and Porto Santo Islands.
Remarks: Not collected in the present study.

Scaphander (Weinkauffia) diaphana Aradas and Maggiore, 1839
Previous records: Watson (1897: 315); Nobre (1937: 14); Nordsieck and García-Talavera (1979: 175 as *Weinkauffia semistriata*), Madeira and Porto Santo Islands.
Remarks: Not collected in the present study.

Roxania utriculus (Brocchi, 1814)
Previous records: Nordsieck and García-Talavera (1979: 170), Madeira Island.
Remarks: Not collected in the present study.

Family SCAPHANDRIDAE G. O. Sars, 1878

Scaphander lignarius (Linné, 1758)
Previous records: Nordsieck and García-Talavera (1979: 171), Madeira Island.
Remarks: Not collected in the present study.

Family PHILINIDAE Gray, 1850

Philine aperta (Linné, 1767)*
Previous records: McAndrew (1852:108); Watson (1897: 303); Nobre (1937: 17); Nordsieck and García-Talavera (1979: 171 as *P. quadripartita*); Linden (1995: 67), Madeira. There are no references for the Selvagens Islands.
Material examined: Madeira, Garajau, 20-100 m depth, 9 specimens (2.7-9.5 mm), (MMF[HN] 30679/30680/30681/30682/30683).
Description: Shell translucent white, with irregular growth lines. This very common species is easily distinguished by the shape of the gizzard plates, which are calcareous and well developed; two are more or less triangular and paired (mirror images of each other), while the third is smaller, narrow, and spindle-shaped. Each plate has two small holes on its outer surface. Radular formula 1.0.1, with hook-shaped teeth provided with more than 40 small denticles along the masticatory edge.

Philine scabra (Müller, 1776)
Previous records: Watson (1897: 303); Nobre (1937: 17), Madeira Island.
Remarks: Not collected in the present study.

Philine catena (Montagu, 1803) (Fig. 3B)
Previous records: Nordsieck and García-Talavera (1979: 171), Madeira. There are no references for the Selvagens Islands.
Material examined: Madeira, Garajau, 75 m depth, one shell (MMF[HN] 31002).
Remarks: We attribute our material to this species on the basis of the microsculpture of the shell, which has transverse striations consisting of several rows of regular indentations, linked together in a chain-like fashion (Fig. 3B).
Watson (1897: 236, pl. 19, figs. 5, 5a) described three new species of *Philine* from Madeira, one of them *P. desmoti,* which specific name means "enchained," with "chain-like" sculpture lines, but whose validity is now difficult to establish, and is only known from Watson's illustration.
Recently Linden (1994) redescribed the species *P. intricata* Monterosato, 1884, based on material from Europe, the Canary Islands, the Azores, and Cape Verde. According to him, the shell sculpture of *P. intricata* resembles that of *P. catena*, although they showed differences, such as the general shape (oval in *P. catena*, square in *P. intricata*), and the spire (narrower in *P. intricata*).

Philine monterosatoi (Vayssière, 1885)
Previous records: Nordsieck (1972: 22, as *Philingwynia monterosati*); Nordsieck and García-Talavera (1979: 171), Madeira and Porto Santo Island.
Remarks: Not collected in the present study.

Philine complanata Watson, 1897
Previous records: Watson (1897: 235); Nobre (1937: 18); Nordsieck and García-Talavera (1979: 172), Madeira Island.
Remarks: Not collected in the present study.

Philine desmotis Watson, 1897
Previous records: Watson (1897: 236); Nobre (1937: 17); Nordsieck and García-Talavera (1979: 172), Porto Santo and Madeira Islands.
Remarks: Not collected in the present study.

Philine trachyostraca Watson, 1897
Previous records: Watson (1897: 236); Nobre (1937: 17); Nordsieck and García-Talavera (1979: 172), Madeira and Porto Santo Islands.
Remarks: Not collected in the present study.

Family AGLAJIDAE Pilsbry, 1895

Melanochlamys maderense (Watson, 1897)*
Previous records: Watson (1897: 238, as *Doridium maderense*); Nobre (1937: 18, as *D. maderense*); Nordsieck and García-Talavera (1979: 172, as *Philine maderense*), Madeira Island.
Remarks: Not collected in the present study.

Aglaja laurentianum (Watson, 1897)
Previous records: Watson (1897: 237); Nobre (1937: 18), Madeira Island.
Remarks: Not collected in the present study.

Chelidonura africana Pruvot-Fol, 1953*
Examined material: Madeira, Porto da Cruz, in a tide pool, one specimen (3 mm long), (MMF[HN] 30097); Quinta do Lorde, in a tide pool, one specimen (2 mm long), (MMF[HN] 30083).
Remarks: This is the first record for the species on Madeira Island.
There is great confusion about the identity of this species relative to *Chelidonura italica* Sordi, 1980. *Chelidonura africana* was first described from the Atlantic shores of Morocco. Later, the status of this species became the object of controversy (Gosliner, 1980; Sordi, 1980; García and García, 1984; Cervera *et al.*, 1988; Martínez *et al.*, 1993; Ortea et al., 1996; Perrone and Sammut, 1997) because the original description by Pruvot-Fol (1953: 31, pl. 3, figs. 37, 38, 39) was not very complete and at least two different species could have been figured by the author (see Gosliner, 1980: 382).
In order to stabilize the nomenclature and avoid further confusion, a detailed history of the problem is given by Martinez *et al.* (2001), who proposed the designation of a

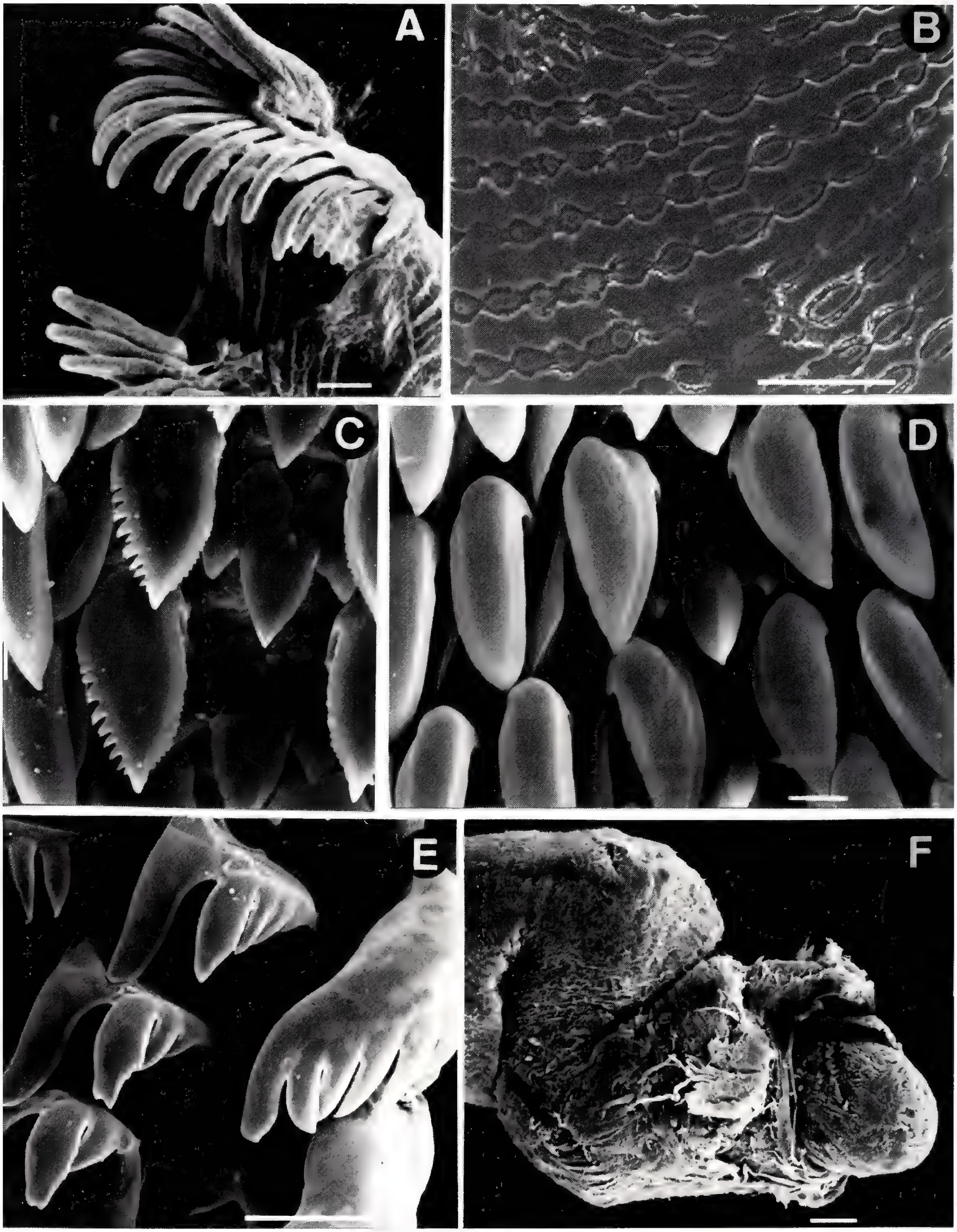


Fig. 3. Scanning electron micrographs. A. *Ringicula conformis*, radular teeth. B. *Philine catena*, detail of shell sculpture. C. *Haminoea orteai*, radular teeth showing rachidian and first lateral tooth. D. *Haminoea hydatis*, radular teeth showing rachidian and first two lateral teeth of each side. E. *Bulla mabillei*, radular teeth showing the two lateral teeth. F. *Bulla mabillei*, penial tip. Scale bars A, C, D = 10 µm; B, E, F = 100 µm.

neotype for *C. africana* and the status of junior subjective synonym for *C. italica*.

Chelidonura sabadiega Ortea, Moro, and Espinosa, 1996*
Examined material: Madeira, Lido, under a stone at 10 m depth, one specimen (6 mm long) (MMF[HN] 30017).
Remarks: This is the first record for the species on Madeira Island.
In the examined specimen the cephalic shield is over half the body length. The posterior shield extends into two thin processes, the left one much longer. There are sensory bristles on each side of the mouth. We attribute our specimen to the species *Chelidonura sabadiega* mainly because of the general shape and color pattern: the general body color is dark purple, with the anterior region of the head and the end of the tail lighter in color. There are two yellow eye-like patches on each side of the anterior end of the cephalic shield. There are also yellow patches on the left posterior process, on the end of the right posterior process, and over the parapodial borders.
Chelidonura sabadiega was recently described by Ortea *et al.* (1996) from specimens obtained at El Hierro, Canary Islands. The species is recorded here for the first time outside of the type locality.

Family RUNCINIDAE H. and A. Adams, 1854

Runcina ornata (Quatrefages, 1844)*
Previous records: Malaquias and Calado (1997, also as *R. adriatica*), Selvagens Islands.
Material examined: Selvagem Grande, Enseada das Cagarras, 8 m depth, one specimen (1 mm long) (MMF[HN] 29785). Madeira: Cais da Junta do Caniçal, intertidal area, two specimens (2-3 mm long) (MMF[HN] 29873). Lazareto, in a tide pool, three specimens (0.9-1.2 mm long).
Description: The ground color of living specimens is uniformly dark brown, with two lighter areas on each side of the head. The eyes are not visible. The dorsal surface of the tail has a narrow dark area that extends to the posterior end of the foot. The sides of the tail are lighter. The body is narrow and elongate.
Remarks: This species lives in eastern Atlantic waters, and has been recorded on the Iberian Peninsula by Cervera *et al.* (1991), who gave a very good diagnosis and described the anatomy.
Malaquias and Calado (1997: 153) labelled several specimens from the Selvagens Islands as *Runcina adriatica* Thompson, 1980, but a subsequent review of this material indicated that this could be a misidentification. More detailed anatomical studies are in progress to clarify this question (Malaquias, pers. comm.).

Family BULLIDAE Lamarck, 1801

Bulla striata Bruguière, 1792
Previous records: Nordsieck (1972: 28 as *Bulla dactylis* Menke, 1853), Madeira Island.
Remarks: Not collected in the present study.

Bulla mabillei Locard, 1896* (Figs. 2F, 3E-F, 4)
Previous records: Watson (1897: 276, as *Bulla punctata* A. Adams, 1868); Nobre (1937: 15 as *B. punctata*); Nordsieck (1972: 28); Nordsieck and García-Talavera (1979: 174), Madeira. Talavera (1978: 126); Nordsieck and García-Talavera (1979: 174); Malaquias and Calado (1997: 154), Selvagens Islands.
Material examined: Madeira, Lido, two empty shells (MMF[HN] 29857). Selvagem Grande, Enseada das Cagarras, five empty shells (26-41 mm long) (MMF[HN] 29786/29794/29795/29914). All the shells were collected on soft substrates, 8-10 m depth. We knew of the presence of living specimens of this species in Madeiran waters from photographs taken by Dr. Peter Wirtz. Because no complete specimens were collected during the *OpisthoMadeira* research program, we dissected one specimen from Barranco Hondo, Tenerife, Canary Islands (35 mm long), collected by Dr. L. Moro (one voucher specimen is available in MMF[HN] 31606).
Description: Our specimens have solid, globose involute shells with a mottled color pattern. Aperture as long as the shell, rising above the vertex, narrow at the upper part and becoming wider toward the base (Fig. 2F). Columella whitish, straight, with a strong base. There are no striae. The shell color varies from violet-pink to purplish-brown, with darker blotches of deep-violet, consistently decorated with white blotches on the right side. Color photographs of living specimens appeared in Sánchez and Batet (1991: 218) and Wirtz (1995: 185).
The dissected specimen has two well-developed posterior processes on the cephalic shield. The radular formula is 30 x 1.2.1.2.1. Rachidian tooth broad, bearing over 10 denticles, the middle one being the shortest. The two lateral teeth (Fig. 3E) are asymmetrical, the second one with a main cusp and bearing about five denticles outside. Marginal teeth plate-like, not denticulated. The strongly muscular gizzard contains three chitinous gizzard plates, identical in shape and similar to those described for other species of this genus, such as *Bulla striata* Bruguière, 1792 and *B. subtropicalis* Powell, 1965 (see Vayssière, 1885; Rudman, 1971). To the right of the buccal mass the penial sheath encloses a smooth penis, which is cylindrical and rounded at the tip (Figs. 3F, 4C). Behind the penial sheath a duct widens into a prostate gland, coiled within a bulbous structure with a well-developed caecum projecting from the end (Figs. 4A-B). The caecum is surrounded by an outer

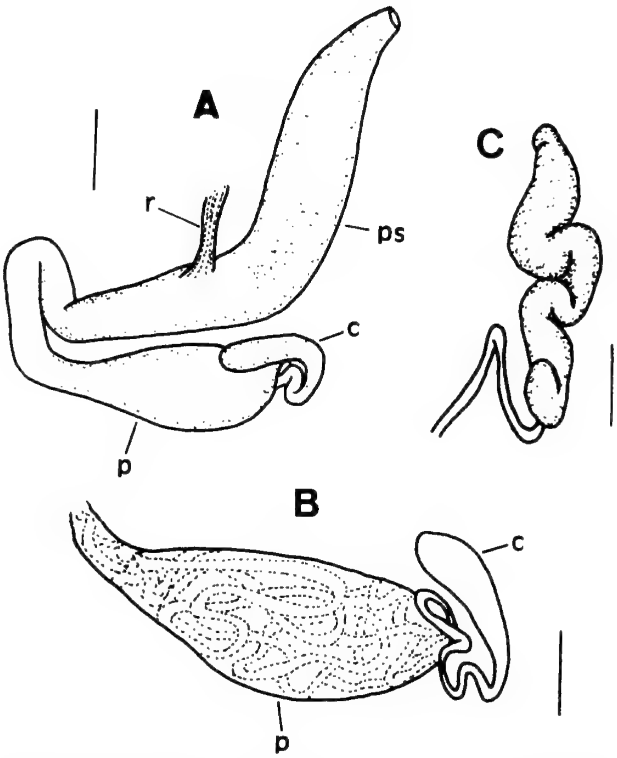


Fig. 4. *Bulla mabillei*, copulatory organ. A. Dorsal view of the penial sheath and prostate gland; scale = 1 mm. B. Detail of the prostate gland, in ventral view, scale = 1.75 mm. C. Diagrammatic anatomy of the penis; scale = 0.5 mm. Abbreviations: c, caecum; p, prostate gland; ps, penial sheath; r, retractor muscle.

muscular layer.

Remarks: Although *Bulla mabillei* is very common in Madeira and the Selvagens Islands, the anatomy of the animal has never been described before.

As with most of the species of *Bulla*, only the shell characteristics of *B. mabillei* have been described previously. Valdés and Héros (1998: fig. 7B) figured one of the two syntypes (currently deposited at the Muséum National d'Histoire Naturelle, Paris), originally described from São Vicente Island, in Cape Verde. The syntype corresponds with our material in both shape and color. This species is mainly known in Cape Verde, the Canary Islands, Madeira and the Selvagens Islands (Odhner, 1932; Marche-Marchad, 1956, 1958; Nordsieck and García-Talavera, 1979; Cosel, 1982a, b; Malaquías and Calado, 1997). Empty shells have also been recorded from Gabon (Bernard, 1984: 108, pl. 54, fig. 216) and the Gulf of Guinea (Marcus and Marcus, 1966: 155).

Watson (1897: 276) recorded the species *Bulla punctata* A. Adams, 1868 in Madeira. Later, Nordsieck and García-Talavera (1979: 174) considered *B. punctata* as a synonym of *B. mabillei*, but without giving any reason for this. These authors also recorded the common Mediterranean and eastern Atlantic species *Bulla striata* Bruguiére, 1789, *B. adansoni* Philippi, 1846, *B. occidentalis* A. Adams, 1855, and *B. amygdala* Dillwyn, 1816 from Madeira and the Canary Islands. However, the validity of some of these species (only known from empty shells) remains doubtful and Pilsbry's (1895: 328) opinion is still valid: "the littoral Bullas of Atlantic waters form a very difficult assemblage, requiring a great mass of material for its elucidation."

Murillo (1996) stated that the morphology of the radula and the prostate gland of *Bulla striata* and other Atlantic species of this genus seem to be very useful characters when separating species. It is obvious that additional anatomical and geographical studies should be carried out on *Bulla*.

Family HAMINOEIDAE Pilsbry, 1895

Haminoea hydatis (Linné, 1758)* (Fig. 3D)

Previous records: Watson (1897: 276 as *Bulla [Haminea] hydatis*); Nobre (1937: 16 as *Haminea hydatis)*; Nordsieck and García-Talavera (1979: 176 as *Haminaea hydatis*), Madeira. Talavera (1978: 126); Malaquias and Calado (1997: 154), Selvagens Islands.

Material examined: Selvagem Grande: Enseada das Cagarras, 3-15 m depth, 11 specimens and six empty shells (2.9-5.1 mm long) (MMF[HN] 30692); Ponta do Leste, five living specimens in shallow waters.

Description: The shell is globose, fragile and translucent, showing delicate growth lines on its surface. In the radula, the innermost lateral tooth is slightly denticulated (Fig. 3D). A useful characteristic to identify this species is the morphology of the prostate gland, which has "a narrow region connecting the two lobes of the gland" (Thompson, 1981: 73). The penis is cylindrical, sharpened towards the tip.

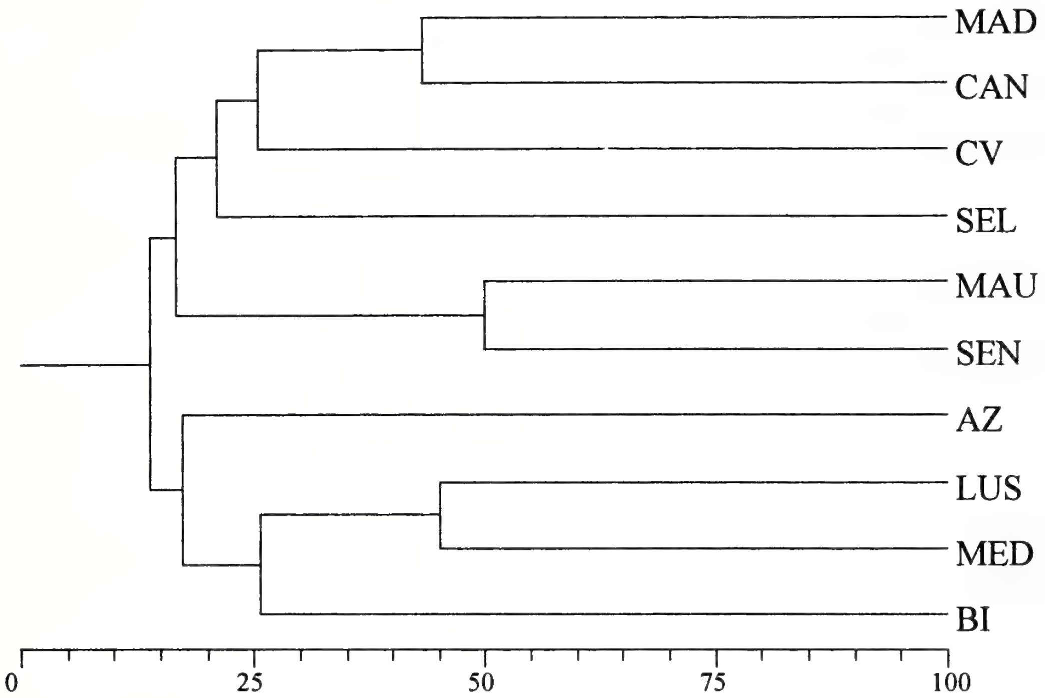
Remarks: A similar morphology of the prostate gland is present in *Haminoea fusari* Álvarez, García, and Villani, 1993, described from Lake Fusaro (Gulf of Naples) and, until now, known only from its type locality. But *H. fusari* shows some anatomical differences with *H. hydatis*, such as the shape of the penis (triangular with a sharpened tip) and the first lateral tooth (smooth and asymmetrically bilobed at the base) (Álvarez *et al.*, 1993: 341).

Haminoea orteai Talavera, Murillo and Templado, 1987* (Fig. 3C)

Previous records: Malaquias and Calado (1997: 154 as *Haminoea* cf. *orteai*), Selvagens Islands.

Material examined: Selvagem Grande, Fonte Salgada, one specimen retracted into the shell (2.5 mm long), found in shallow waters (MMF[HN] 30684).

Description: The studied specimen is a juvenile, without fully developed genital structures. The prostate gland has



	MAD	CV	AZ	SEL	CAN	LUS	MED	BI	MAU	SEN
MAD	100									
CV	25	100								
AZ	14	17	100							
SEL	23	17	9	100						
CAN	43	26	14	23	100					
LUS	31	14	21	8	24	100				
MED	23	12	20	8	22	45	100			
BI	19	7	11	7	14	28	23	100		
MAU	22	15	10	9	17	19	14	11	100	
SEN	20	18	7	15	17	12	8	12	50	100

Fig. 5. Dendrogram and matrix of similarity depicting biogeographical affinities between the cephalaspideans from Madeira (MAD), Selvagens (SEL), Canary Islands (CAN), Azores (AZ), Cape Verde (CV), British Isles (BI), Mediterranean Sea (MED), Lusitania (LUS), Mauritania (MAU) and Senegal (SEN) (Jaccard similarity index, values are in percentage).

two lobes, the proximal one smaller than the distal. Penis small, having an apical crest. The first lateral tooth of the radula is denticulated on both edges, the denticles of the outer margin being more developed (Fig. 3C), as Mikkelsen (1995: 201) described for Azorean specimens.
Remarks: Since its original description in the Mediterranean by Talavera *et al.* (1987) (type locality Salinas del Rasall, Murcia, southeast Spain), this species has been recorded in the Gulf of Naples (Villani and Martínez, 1993), Azores (Mikkelsen, 1995, as *H. cf. orteai*), and Selvagens Islands (Malaquías and Calado, 1997, also as *H. cf. orteai*). The species is also known from the Canary Islands, Cape Verde and the Atlantic coast of Morocco (unpublished data).

Atys jeffreysi (Weinkauff, 1868)
Previous records: Nobre (1889: 16; 1937: 15, as *Roxaniella jeffreysi*); Watson (1897: 274); Nordsieck and García-Talavera (1979: 175, as *A. [Roxaniella] jeffreysi*), Madeira Island.
Remarks: Not collected in the present study.

Atys macandrewii E. A. Smith, 1872*
Previous records: Nordsieck (1972: 30 as *Atys [Limulatys] macandrewi*), Madeira. Talavera (1978: 126); Malaquias and Calado (1997: 154), Selvagens Islands.
Material examined: Madeira, Lido, 22 m depth, one living specimen; Garajau, 20-100 m depth, 19 empty shells (MMF[HN] 30687/30688/30693/30701). Selvagem Grande, Ponta da Atalaia, 18 m depth, on sandy substrate, one living specimen.
Description: The shell is involute, oval to elongated, translucent with opaque white bands. This species has been recently redescribed by Martínez and Ortea (1998), who gave details on shell variability and described the radula, jaws, and gizzard plates. These data agree with the specimens collected on Madeira and the Selvagens Islands.

DISCUSSION

Thirty-seven species of cephalaspidean opisthobranchs have been recorded from Madeira and the Selvagens Islands in the literature. Most of these species were described or identified from empty shells and were apparently never collected alive (or, at least, not recorded as such).

In the *OpisthoMadeira* project a total of 14 species from Madeira and the Selvagens were collected and studied in detail. Two of them, belonging to the family Aglajidae, *Chelidonura africana* and *Chelidonura sabadiega*, are recorded for the first time in this area. This is also the first reference to the genus *Chelidonura* A. Adams, 1850 in Madeira Island.

With the present study, the number of cephalaspideans recorded from Madeira and the Selvagens increases to 38 species, 12 of them collected alive (*Ringicula conformis, Retusa* sp., *Philine aperta, Chelidonura africana, C. sabadiega, Runcina ornata, Bulla mabillei, Haminoea hydatis, H. orteai*, and *Atys macandrewii*). More than half of these occurrences were first reported in the 19th century, and later repeated in several malacological papers.

Additional research needs to be carried out on the cephalaspideans from Madeira, with two main objectives. First of all to confirm the presence of the species mentioned in earlier literature whose identifications were based on empty shells from dead specimens. Second to redescribe the species originally described from Madeira (and still known only from Madeira) whose anatomy remain unknown, as is the case of *Pyrunculus spretus, Philine complanata, P. desmotis, P. trachyostraca, Diaphana flava*, and *Aglaja laurentianum*.

Affinity of the cephalaspidean fauna from Madeira and Selvagens with that of other localities

According to the similarity analysis, the area with the greatest affinity to Madeira is the Canary islands (43%), followed by the Lusitanean region (31%), Cape Verde (25%) and Mauritania (22%). The Selvagens Islands and the Mediterranean Sea have the same degree of similarity with Madeira (23%). Senegal (20%) and the British Isles (19%) have a slightly lower similarity. The Azores are the least similar (14%).

Although several works on marine zoogeography have been written (e.g. Ekman, 1953; Briggs, 1974), it is clear that there are differences of opinion regarding the classification and treatment of corresponding zoogeographical categories (López-González, 1993). The faunistic affinities of the opisthobranch molluscs from Madeira and, in general, from the Macaronesian Islands, are not well known and work is in progress in this field. Meanwhile, the similarity analysis (Fig. 5), shows the existence of two principal groups, with a clear discrimination between the cephalaspideans from Mauritania, Senegal, and the Macaronesian Archipelagos (except the Azores) on one side, and Lusitania and the Mediterranean, together with the British Isles and the Azores on the other. Within the first group the high affinity between the fauna of Madeira and the Canary Islands (43%) is notable. The percent similarities of these faunas with those of relatively close areas, such as the Selvagens, Cape Verde, Mauritania, and Senegal are low. Differences in the levels of knowledge on the various zones could be contributing to the differences found. Additionally we must point out the high similarity between the faunas of the continental shores of Mauritania and Senegal (50%).

The low similarity (14%) of the cephalaspideans from Madeira and the Azores is also noteworthy. Ecological causes related to larval dispersal and/or physical factors such as surface currents and water temperature could contribute to these results. Mikkelsen (1995) also found a greater similarity between the cephalaspideans of the Azores and the European-Mediterranean area than between the Azores and Madeira. Similar results have been obtained by Ávila (2000) in studies on shallow-water molluscs from the Azores.

Several authors have considered the Azores and Madeira as part of the Macaronesian biogeographical region, together with Cape Verde, Selvagens, and the Canary Islands (Sunding, 1979; Mitchell-Thomé, 1976; Beyhl, 1995; Beyhl *et al.*, 1995; Sjögren, 2000). But this common view is misleading, and the biogeographically homogenous entity "Macaronesia" is accepted as topographic nomenclature without any biogeographic meaning (Beyhl *et al.*, 1995). Our results are also consistent with this perspective and suggest the existence of a boundary between the Azores and Madeira that makes those archipelagoes more similar to the Lusitanian and Mediterranean regions than to each other.

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APPENDIX.

Presence / absence data matrix for similarity analysis for Madeira and the other indicated geographic areas (0 - absence and 1 - presence).

Spp./Locality	Madeira	Cape Verde	Azores	Selvagens	Canary Is.	Lusitanean Region	Mediter-ranean	British Is.	Mauritania	Senegal
Japonacteon pusillus	1	1	1	0	0	1	1	0	0	0
Pseudacteon luteofasciatus	0	0	0	0	0	0	1	0	0	0
Ovulacteon meeki	0	0	1	0	0	0	0	0	0	0
Acteon tornatilis	1	0	0	0	0	1	1	1	1	1
=Pupa candidula										
=Pseudacteon augustoi										
Acteon incisus	0	0	1	0	0	0	0	0	0	0
Acteon senegalensis									1	1
Acteon maltzani									1	1
Acteon monterosatoi	0	0	1	0	0	1	1	0	1	0
Acteonina chariis	0	0	1	0	0	0	0	0	0	0
Acteocina protracta	0	0	1	0	0	0	0	0	0	0
Acteocina mueromata	0	1	0	0	0	0	0	0	1	1
=Acteocina knockeri										
Colostracon amabile	1	0	1	0	1	0	0	0	0	0
Crenilabium exile	0	0	1	0	0	1	1	0	0	0
Inopinodon azoricus	0	0	1	0	0	0	0	0	0	0
Ringicula auriculata	1	0	0	0	1	1	1	0	1	0
Ringicula conformis	1	1	0	0	0	1	1	0	1	0
Ringicula someri	1	1	0	0	1	1	0	0	0	0
Ringicula leptocheila	0	0	1	0	0	1	1	0	1	0
=Ringicula blanchiardi										
=Ringicula nitida										
=Ringicula pirulina										
=Ringicula minutula										
Ringicula semistriata	0	0	1	0	0	0	0	0	0	0
Ringicula buccinea	0	0	0	0	0	1	1	0	0	0
Ringicula abyssorum	0	0	0	0	0	0	1	0	0	0
Hydatina physis	1	1	1	0	1	0	0	0	1	1
Hydatina velum	0	0	0	0	1	0	1	0	0	0
Diaphana minuta	1	0	0	0	1	1	1	1	0	0
Diaphana expansa	0	0	0	0	0	0	0	1	0	0
Diaphana flava	1	0	0	0	0	0	0	0	0	0
Diaphana seguenzae	0	0	1	0	0	0	0	0	0	0
Diaphana hiemalis	0	0	0	0	0	1	0	0	0	0
Diaphana cretica	0	0	0	0	0	0	1	0	0	0
Diaphana ventrosa	0	0	0	0	0	0	1	0	0	0
Diaphana quadrata	0	0	0	0	0	0	1	0	0	0
Diaphana lactea	0	0	0	0	0	0	1	0	0	0
Colpodaspis pusilla	0	0	0	0	0	0	0	1	0	0
Colobochephalus striatulus	0	0	0	0	0	0	1	0	0	0
Retusa truncatula	1	0	1	1	1	1	1	1	1	1
=Retusa semisulcata										
Retusa minutissima									1	0
Retusa leptoeneilema	1	0	0	1	1	0	1	0	0	0
Retusa mammillata	1	0	0	1	1	1	1	0	1	1
Retusa tornata	1	0	0	0	1	1	0	0	0	0
Retusa multiquadrata	0	0	1	0	0	0	1	0	0	0
Retusa leuca	0	0	1	0	0	0	0	0	0	0
Retusa obtusa	0	0	0	0	0	1	1	1	0	0
Retusa pellucida	0	0	0	0	0	1	1	0	0	0
Retusa piriformis	0	0	0	0	0	0	1	0	0	0
Retusa truncatella	0	0	0	0	0	1	1	0	0	0
Retusa pusillina	0	0	0	0	0	1	0	0	0	0
Retusa fourierii	0	0	0	0	0	0	1	0	0	0
Retusa candidula	0	0	0	0	0	0	1	0	0	0
Retusa obesa nome nudum										

(continued)

APPENDIX (continued)

Presence / absence data matrix for similarity analysis for Madeira and the other indicated geographic areas (0 - absence and 1 - presence).

Spp./Locality	Madeira	Cape Verde	Azores	Selvagens	Canary Is.	Lusitanean Region	Mediterranean	British Is.	Mauritania	Senegal
Cylichnina umbilicata	1	0	1	0	0	1	1	1	0	0
Cylichnina nitidula	1	0	0	0	0	1	1	0	0	0
Cylichnina robagliana	0	0	0	0	0	1	0	0	0	0
Cylichnina crebrisculpta	0	0	0	0	0	1	1	0	0	0
Cylichnina laevisculpta	0	0	0	0	0	0	1	0	0	0
Cylichnina canariensis	0	0	0	0	1	0	0	0	0	0
Cylichnina tenerifensis	0	0	0	0	1	0	0	0	0	0
Cylichna alba	0	0	1	0	0	1	1	1	0	0
Cylichna chevreuxi	0	0	1	0	0	0	0	0	0	0
Cylichnium oliviforme	0	0	1	0	0	1	0	0	0	0
Pyrunculus ovatus *=Cylichna ovata*	0	0	1	0	0	1	1	0	0	0
Pyrunculus spretus *=Cylichna spreta*	1	0	0	0	0	0	0	0	0	0
Pyrunculus hoernesii *=Retusa striatula*	0	0	0	0	0	0	0	0	1	0
Pyrunculus minutissimus	0	0	0	0	0	0	1	0	0	0
Cylichna piettei	0	0	1	0	0	0	0	0	0	0
Cylichna cylindracea	1	1	1	0	1	1	1	1	1	1
Cylichna crossei	0	0	0	0	0	0	1	0	0	0
Cylichna propecylindracea	0	0	0	0	1	0	1	0	0	0
Cylichna fischeri	0	0	0	0	0	1	0	0	0	0
Cylichna mirabilis	0	0	0	0	0	1	1	0	0	0
Cylichna striatula	0	0	0	0	0	1	1	0	0	0
Cylichna parvula	0	0	0	0	0	0	1	0	0	0
Cylichnium africanum	0	0	0	0	0	1	0	0	0	0
Mamillocylichna richardi	0	0	1	0	0	1	0	0	0	00
Rhizorus acuminatus	0	0	0	0	0	1	1	1	0	0
Volvula acuminata	0	0	0	0	0	0	0	0	1	1
Scaphander lignarius	1	0	0	0	1	1	1	1	0	0
Scaphander punctostriatus	0	0	1	0	0	1	1	1	0	0
Scaphander (W.) diaphana	1	0	0	0	0	0	0	0	1	1
Scaphander gracilis	0	0	1	0	0	0	1	0	0	0
Scaphander nobilis *=Bulla millepunctata*	0	0	1	0	0	1	0	0	0	0
Philine aperta	1	1	0	0	0	1	1	1	1	1
Philine scabra	1	0	0	0	1	1	1	1	1	0
Philine catena	1	0	0	0	1	1	1	0	0	0
Philine monterosatoi	1	0	0	0	0	1	1	0	0	0
Philine complanata	1	0	0	0	0	0	0	0	0	0
Philine desmotis	1	0	0	0	0	0	0	0	0	0
Philine trachyostraca	1	0	0	0	0	0	0	0	0	0
Philine approximans	0	0	1	0	0	0	0	0	0	0
Philine azorica	0	0	1	0	0	0	0	0	0	0
Philine lima	0	0	1	0	0	1	1	0	0	0
Philine monilifera	0	0	1	0	0	0	0	0	0	0
Philine quadrata	0	0	1	0	0	1	1	0	0	0
Philine rugulosa	0	1	1	0	0	0	0	0	0	0
Philine intricata	0	1	1	0	0	0	1	0	0	0
Philine punctata	0	0	0	0	0	1	1	0	0	0
Philine calva	0	0	1	0	0	0	0	0	0	0
Philine condensa	0	0	1	0	1	0	0	0	0	0
Philine denticulata *=Philinorbis sinuata*	0	0	0	0	0	0	1	1	0	0
Philine araneosa	0	1	0	0	0	0	0	0	0	0
Philine milneedwardsi	0	1	0	0	0	0	0	0	0	0

(continued)

APPENDIX (continued)

Presence / absence data matrix for similarity analysis for Madeira and the other indicated geographic areas (0 - absence and 1 - presence).

Spp./Locality	Madeira	Cape Verde	Azores	Selvagens	Canary Is.	Lusitanean Region	Mediter-ranean	British Is.	Mauritania	Senegal
Rhinodiaphana ventricosa *=Philine cf. ventricosa*	0	1	0	0	0	0	0	0	0	0
Philiniorbis angulata	0	0	0	0	0	0	1	1	0	0
Philiniorbis vitrea	0	0	0	0	0	0	1	0	0	0
Johania retifera	0	0	0	0	0	0	1	0	0	0
Laona flexuosa	0	0	0	0	0	0	1	0	0	0
Laona pruinosa	0	0	0	0	0	0	1	0	0	0
Gastropteron meckeli	0	0	0	0	0	1	1	0	0	0
Philinoglossa helgolandica	0	0	0	0	0	1	1	1	0	0
Philinoglossa remanei	0	0	0	0	0	0	1	0	0	0
Philinoglossa praelongata	0	0	0	0	0	0	1	1	0	0
Philinoglossa latosoleata	0	0	0	0	0	0	1	0	0	0
Melanochlamys maderense	1	1	0	0	1	0	0	0	0	0
Melanochlamys seurati	0	0	0	0	0	0	1	0	0	0
Aglaja laurentianum	1	0	0	0	0	0	0	0	0	0
Aglaja tricolorata	0	0	0	0	1	0	1	0	0	0
Aglaja berrieri	0	0	0	0	0	0	1	0	0	0
Aglaja taila	0	0	0	0	0	0	1	0	0	0
Aglaja minuta	0	0	0	0	0	0	0	0	1	0
Philinopsis depicta *=Aglaja coriacea*	0	1	0	0	1	0	1	0	0	0
Runcina ornata	1	0	0	1	0	0	0	0	0	0
Runcina coronata	0	0	1	0	0	1	1	1	0	0
Runcna adriatica	1	0	1	0	0	0	1	0	0	0
Runcina bahiensis	0	0	0	0	0	1	0	0	0	0
Runcina ferruginea	0	0	0	0	0	1	1	1	0	0
Runcina capreensis	0	0	0	0	0	0	1	0	0	0
Runcina falciforme	0	1	0	0	0	0	0	0	0	0
Runcina paupera	0	1	0	0	0	0	0	0	0	0
Runcina africana	0	0	0	0	0	0	0	0	1	0
Bulla mabillei *=Bulla amygdala*	1	1	0	1	1	1	1	0	0	0
Bulla striata *=Bulla roperiana* *=Bulla dactylis* *=Bulla occidentalis* *=Bulla adansoni*	1	1	1	1	1	1	1	0	1	1
Bulla utriculata	0	0	0	0	0	0	0	0	1	0
Bulla semilaevis incertae sedis										
Haminoea hydatis	1	1	1	1	1	1	1	1	0	0
Haminoea elegans	0	0	0	0	0	0	0	0	1	0
Haminoea orteai	1	1	1	1	1	0	1	0	0	0
Haminoea navicula	0	0	0	0	0	1	1	1	0	0
Haminoea orbignyana	0	1	0	0	1	1	1	0	1	1
Haminoea cymoelia	0	0	0	0	0	0	1	0	0	0
Haminoea templadoi	0	0	0	0	0	1	0	0	0	0
Haminoea gantesae	0	0	0	0	0	0	0	0	1	0
Haminoea temarana	0	0	0	0	0	0	0	0	1	0
Atys jeffreysi	1	1	0	0	0	1	1	0	0	0
Atys macandrewi	1	1	1	1	1	0	0	0	0	0
Atys blainvilliana	0	0	0	0	0	0	1	0	0	0
Smaragdinella algirae	0	0	0	0	0	0	1	0	0	0
Weinkauffia turgidula	0	0	0	0	1	1	1	0	0	0
Weinkauffia semistriata	0	0	0	0	1	1	1	0	0	0
Meloscaphander imperceptus	0	0	1	0	0	0	0	0	0	0
Roxania utriculus	1	0	0	0	1	1	1	1	0	0

(continued)

APPENDIX (continued)

Presence / absence data matrix for similarity analysis for Madeira and the other indicated geographic areas (0 - absence and 1 - presence).

Spp./Locality	Madeira	Cape Verde	Azores	Selvagens	Canary Is.	Lusitanean Region	Mediterranean	British Is.	Mauritania	Senegal
Roxania monterosatoi	0	0	1	0	0	0	1	0	0	0
Roxania pinguicula *=Bulla pinguicula* *=Bulla guernieri*	0	0	1	0	0	1	1	0	1	0
Chelidonura sabadiega	1	0	0	0	1	0	0	0	0	0
Chelidonura africana	1	0	0	0	1	1	1	0	1	1
Chelidonura leopoldoi	0	0	0	0	1	0	0	0	0	0
Chelidonura fulvipunctata	0	0	0	0	0	0	1	0	0	0
Licarenus globulinus	0	0	1	0	0	0	1	0	0	0
Mysouffa turritus	0	0	1	0	0	0	0	0	0	0
Micromelo undatus	0	1	1	0	1	0	0	0	0	0
Relichna simplex *=Bulla simplex*	0	1	1	0	0	0	0	0	0	0

A new subgenus and two new species of *Canariella* Hesse, 1918 (Gastropoda: Pulmonata: Hygromiidae)*

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Abstract: Two new species of *Canariella*, *Canariella ronceroi* n. sp. from La Gomera Island and *C. bimbachensis* n. sp. from El Hierro Island (Canary Islands, Atlantic Ocean), assigned to the new subgenus *Gara* are described. The new subgenus is characterized by the following synapomorphies of its species: "Penis wall with a thickened ring-shaped portion" and "penis with a toughened distal anklebone-like penial pilaster portion." The extinct species *C. pontelirae* Hutterer, 1994 also belongs to *Gara* n. subgen.

Key Words: Taxonomy, conservation, Canary Islands, new taxa

All recent species of the genus *Canariella* Hesse, 1918 are endemic to the Canary Islands, one of the Macaronesian archipelagoes. Species of *Canariella*, as well as other Canarian endemics, have generally small distribution areas restricted to one island, and only *C. plutonia* (Lowe, 1861) is found in two islands.

Ten living species (19 nominal taxa of specific and subspecific rank) of *Canariella* are recognized as valid. One of them belongs to the subgenus *Canariella*: *C. hispidula* (Lamarck, 1822), from Tenerife. Three other species belong to the subgenus *Alvaradoa* Ibáñez and Alonso, 1994 (Groh *et al.*, 1994): *C. pthonera* (Mabille, 1883), from Tenerife, *C. multigranosa* (Mousson, 1872), from La Gomera, *C. huttereri* Ponte-Lira and Groh, 1994, from El Hierro. An additional species, *C. plutonia* Lowe, 1861, from Lanzarote and Fuerteventura, belongs to the subgenus *Simplicula* Ponte-Lira and Alonso, 1996 (Ponte-Lira *et al.*, 1996), and it is the largest species of the genus (shell height: 16.5 mm; shell diameter: 27 mm).

The remaining five species: *Canariella planaria* (Lamarck, 1822), from Tenerife, *C. leprosa* (Shuttleworth, 1852), from Tenerife, *C. discobolus* (Shuttleworth, 1852), from La Gomera, *C. eutropis* (Shuttleworth in Pfeiffer, 1860), from Fuerteventura, and *C. gomerae* (Wollaston, 1878), from La Gomera, have not been arranged in subgenera (Ibáñez *et al.*, 1995), because some of them will be grouped with other not yet described species.

Additionally, one extinct species from Tenerife, *Canariella pontelirae* Hutterer, 1994, and some other fossils from Lanzarote Island (Gittenberger and Ripken, 1985) and Europe (Pfeffer, 1929; Wenz, 1924; Zilch, 1960) have been assigned to *Canariella*.

In this paper we describe two additional species of *Canariella*, one of them collected from La Gomera and the other one from El Hierro, the youngest (1.1 My old), smallest (278 km^2), and westernmost island of the Canarian archipelago. Both species are assigned to the new subgenus *Gara*, which also includes the extinct species *Canariella pontelirae*, whose similarity to the new species was indicated by Hutterer (1994).

METHODS

The biometric methodology used in the conchological descriptions is the same as Ibáñez *et al.* (1995). Calculation of number of shell whorls follows Kerney *et al.* (1979). The terms "shell" and "specimen" refer to empty shells and live specimens respectively, and "proximal" and "distal" refer to the position in relation to the gonad.

Abbreviations

AIT: M. Alonso and M. Ibáñez collection, Departamento de Biología Animal, Universidad de La Laguna, Tenerife, Canary Islands, Spain
CHB: R. Hutterer private collection, Bonn, Germany
CRT: W. Rähle private collection, Tübingen, Germany
MNHN: Muséum National d'Histoire Naturelle, Paris, France
NHM: The Natural History Museum, London, UK

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NMW: National Museum of Wales, Cardiff, UK
NNM: Nationaal Natuurhistorisch Museum, Leiden, The Netherlands
SMF: Natur-Museum Senckenberg, Frankfurt/Main, Germany
TFMC: Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain

TAXONOMIC DESCRIPTIONS

Family Hygromiidae Tryon, 1866
Genus *Canariella* Hesse, 1918
Type species *Carocolla hispidula* Lamarck, 1822, by monotypy.

Diagnosis

Mantle collar with five lobes, left lateral lobe almost indistinguishable in several species. Kidney sigmurethric, without secondary ureter. Central and first lateral radular teeth with small but visible ectocones. Right ommatophore retractor passing between penis and vagina. Dart-sac complex absent. One or several crown-shaped vaginal glands, each with an independent, slender initial portion present. Distal male duct, between atrium and penial retractor muscle insertion, with a sheath. Differentiation of penis and epiphallus indistinguishable externally. Penial retractor muscle with an epiphallar insertion. Penial nerve originating from right cerebral ganglion.

Subgenus *Gara* Alonso and Ibáñez, new subgenus
Type species *Canariella ronceroi* new species

Diagnosis

Penis without penial papilla, with an eccentric orifice connecting the epiphallus, and with a thick longitudinal pilaster opposite to the penis retractor muscle insertion. Penial pilaster with two portions, a soft proximal short ending in the epiphallus and an anklebone-like toughened long distal section. Penis wall with a thickened ring-shaped portion joined to the distal penial pilaster portion. Epiphallar longitudinal folds ending distally as small papillae on the orifice connecting the penis. One of the papillae situated over the proximal pilaster portion. Vagina with longitudinal folds and a digitiform vaginal gland.

Remarks

Gara n. subgen. differs from all the other *Canariella* taxa mainly by the presence of the following synapomorphies in all species described: "Penis wall with a thickened ring-shaped portion," and "penis with an anklebone-like toughened distal penial pilaster portion."

Etymology

The name of the Garajonay National Park derives from Gara and Jonay, two ancient lovers from La Gomera Island. The name of the new subgenus is dedicated to the beautiful Gara.

Canariella (Gara) ronceroi Ponte-Lira, new species

(Figs. 1A-B, 2A)

Type material

HOLOTYPE: AIT (no registration numbers used), 1 February 1989, leg. F. C. Henríquez, E. Ponte-Lira and M. J. Valido.

PARATYPES: 144 specimens and 22 shells collected between 1985 and 1994: AIT, MNHN, NMW (Z.1992.089.02/1), NHM (1993052/1), NNM (56865/1), SMF (309932/1), TFMC (MT 0284/1).

Type locality

Playa de Vallehermoso (La Gomera; UTM: 28RBS7921, 50 m altitude).

Description

Body whitish-gray, head with longitudinal lines of small darker gray spots. Shell discoidal, with a nearly flat spire of 5 - 5 1/2 strongly keeled, slightly overlapping whorls; umbilicus large (larger than 22% shell diameter), eccentric. Aperture ovate, with a small notch at the keeled periphery and a very thin parietal thickening in old specimens. Basal and collumelar peristome regions slightly reflected. Color uniform matt whitish-brown. Teleoconch with prominent and regularly-spaced radial ribs separated by 4 - 5 small ribs; ribs crossed by delicate spiral lamellae, visible under magnification. Protoconch small and only faintly striated. Periostracal hairs, abundant and long (up to 700 μm long) on the keel, fewer and slightly shorter on the suture, and abundant and very short (< 55 μm long) on the umbilicus.

Genital system

Six specimens dissected. Atrium short. Distal male duct similar in length to the epiphallar proximal portion; flagellum very short and slender. Distal male duct with a short sheath, joining distally to the penis halfway down. Penis distally widened with anklebone-like pilaster portion occupying 3/4 of penis length. Ring-shaped penis, wall portion narrow and joined to central zone of the distal penial pilaster portion. Epiphallus with four longitudinal folds.

Tubular vagina shorter than the penis, with numerous small longitudinal folds, the majority converging proximally into the oviduct; vaginal gland opening near the orifice connecting to the oviduct. Distal bursa copulatrix duct with numerous irregular longitudinal folds.

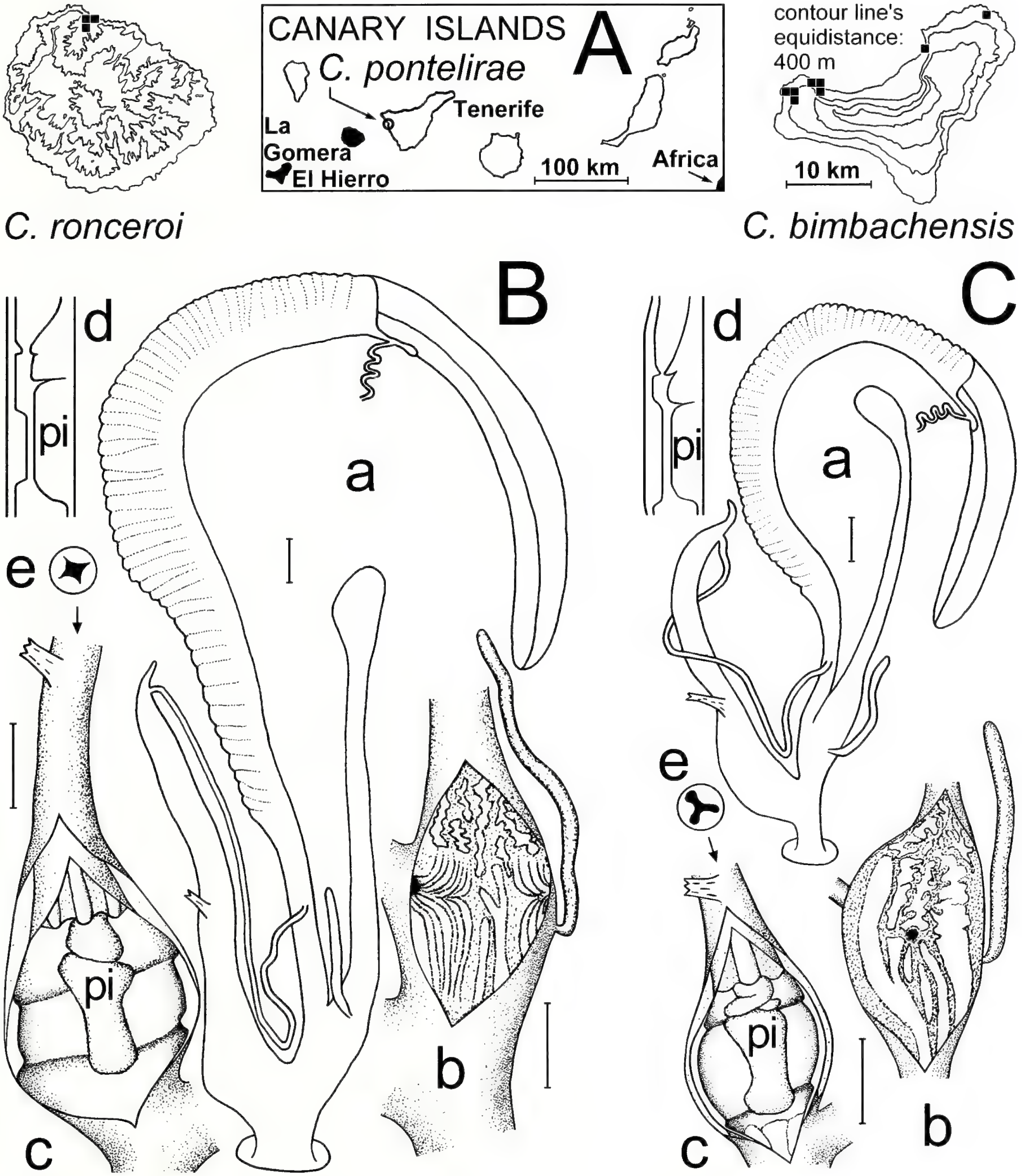
C. ronceroi
CANARY ISLANDS
A
C. pontelirae
Tenerife
La Gomera
El Hierro
100 km
Africa
contour line's equidistance: 400 m
10 km
C. bimbachensis
B
d
pi
a
e
c
b
C
d
pi
a
e
c
b

Fig. 1. A. Geographical distribution of the species of *Gara*; the symbols represent 1 x 1 km squares. **B.** Genital system and anatomical details of *Canariella (Gara) ronceroi* n. sp., from Playa de Vallehermoso, La Gomera. **C.** Genital system and anatomical details of *C. (Gara) bimbachensis* n. sp., from Las Lajas, El Hierro. Scale bar = 1 mm. Abbreviations: a, genital system; b, vagina; c, penis; d, diagram of a penial longitudinal section (without scale); e, transverse section of epiphallus; pi, pilaster.

Distribution, habitat, and conservation status

This species is endemic to north of La Gomera, occurring in a very small area of about 4 km^2 with lowland vegetation, at an altitude between 30 and 100 m. Conservation status proposed: "Endangered" (EN, B1, B2c), according to the IUCN (1994, 1996) Red List categories.

Etymology

The specific name is dedicated to Dr. Octavio Roncero, Madrid (C. E. Ponte-Lira's husband).

Canariella (Gara) bimbachensis Ibáñez and Alonso, new species

(Figs. 1A,C, 2B)

Type material

HOLOTYPE: AIT (no registration numbers used), 19 January 1989, leg. F. C. Henríquez, E. Ponte-Lira and M. J. Valido.

PARATYPES: 2 specimens and 74 shells collected between 1984 and 1997: AIT, CHB, CRT, TFMC (MT 0285/1).

Type locality

Las Lajas (El Hierro; UTM: 28RBR0578, 20 m altitude).

Description

Shell discoidal, with a flattened spire, moderately domed above and rather flattened below, of 5 - 5 3/4 keeled, slightly overlapping whorls; umbilicus large (larger than 18% shell diameter). Aperture ovate, with a small notch at the keeled periphery and a wide parietal zone. Basal and

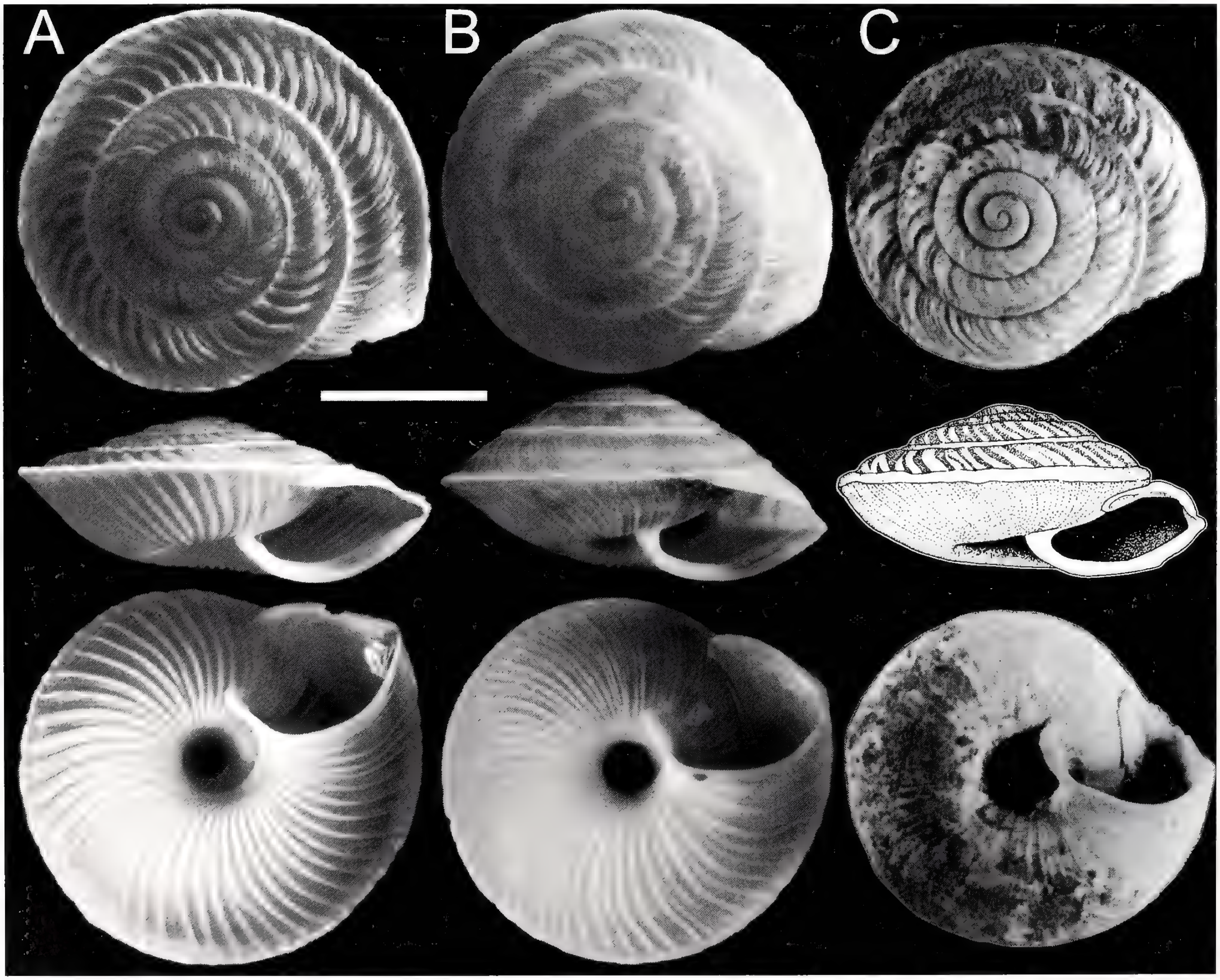

Fig. 2. Holotype shells. **A.** *Canariella (Gara) ronceroi* n. sp. **B.** *C. (Gara) bimbachensis* n. sp. **C.** *C. (Gara) pontelirae*. Scale bar = 5 mm.

collumelar peristome regions slightly reflected. Color uniform matt whitish-brown. Teleoconch with regularly-spaced radial ribs separated by 4 - 5 small ribs; ribs crossed by delicate spiral lamellae, visible under magnification. Protoconch small and only faintly striated. Periostracal hairs abundant and up to 600 µm long on the keel, apparently absent on the suture, and abundant and very short (< 50 µm long) on the umbilicus.

Genital system

Only 1 specimen dissected. Atrium short. Distal male duct similar in length to the epiphallar proximal portion; flagellum short and slender. Distal male duct with a sheath covering all its length. Penis widened with ankle-bone-like pilaster portion occupying nearly all the penis length. Ring-shaped penis wall portion wide and joined to almost all the distal penial pilaster portion. Epiphallus with three longitudinal folds.

Vagina proximally widened, shorter than penis, with several longitudinal folds; vaginal gland opening near the orifice connecting with oviduct. Distal bursa copulatrix duct with several irregular longitudinal folds.

Distribution, habitat, and conservation status

A species endemic to the northwest of El Hierro, occurring in an area of about 50 km^2 with partially degraded lowland vegetation, at an altitude between 20 and 350 m. Conservation status proposed: "Vulnerable" (VU, B1, B2c).

Etymology

The specific name derives from "bimbaches," the name of the first inhabitants from El Hierro Island.

Remarks

Canariella ronceroi n. sp. differs from *C. bimbachensis* n. sp. as follows: the shell is larger, flatter, with stronger teleoconch ornamentation and an eccentric umbilicus; the penis has a narrower ring-shaped thickened wall portion and a shorter distal pilaster portion, the last occupying only 3/4 of the penis length; the sheath surrounding the distal male duct is shorter, joining distally to halfway down the penis; the epiphallus has four longitudinal folds (Table 1).

We also include in the new subgenus the extinct species *Canariella pontelirae* (Figs. 1A, 2C) due to the resemblance of the shape and ornamentation of the shell with the two new species. The shell of *C. pontelirae* has the A/B index similar to that of *C. bimbachensis* n. sp. but the upper side is flatter than that of *C. bimbachensis* n. sp., occupying an intermediate position between *C. bimbachensis* n. sp. and *C. ronceroi* n. sp. The shell aperture of *C. pontelirae* is flatter than that of the two new species, and the shell ornamentation of the upper side of *C. pontelirae* is as protuberant as that of *C. ronceroi* n. sp. whereas the lower side of *C. pontelirae* has an ornamentation as protuberant as that of *C. bimbachensis* n. sp.

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Table 1. Biometric data (dimensions in mm) and indices of the shell of the species of *Gara*. Abbreviations: A, shell height; B, shell diameter; C, shell body whorl height; CV, Pearson's variation coefficient (in %); D, shell height, ventral side; E, length of shell aperture; F, width of shell aperture; G, umbilicus diameter (without the peristome); H, shell height, dorsal side (= A-D); M, maximum value; m, minimum value; n, number of measured specimens; X, average.

	A	B	C	D	E	F	G	A/B	H/B	D/B	E/F	B/G	n
Canariella ronceroi n. sp.													
	5.16	12.88	4.14	3.23	4.91	5.85	3.21	(holotype)					
M	5.69	13.48	4.37	3.95	5.22	6.00	3.42						
m	4.56	11.26	2.95	3.14	4.42	5.19	2.34						
X	5.06	12.60	3.94	3.56	4.82	5.65	2.84	0.40	0.12	0.28	0.85	4.47	30
CV	4.31	3.03	6.11	4.74	3.01	2.82	6.36	4.36	15.94	5.07	3.04	6.92	
Canariella bimbachensis n. sp.													
	5.87	11.75	4.41	3.12	4.72	5.35	1.97	(holotype)					
M	5.87	13.05	4.50	3.59	4.98	5.67	2.55						
m	5.51	11.35	4.08	3.12	4.13	4.73	1.82						
X	5.64	12.04	4.31	3.35	4.72	5.33	2.21	0.47	0.19	0.28	0.89	5.50	7
CV	1.86	4.75	2.71	3.71	3.59	3.72	8.98	4.49	8.13	5.40	1.42	8.53	
Canariella pontelirae Hutterer, 1994 (data from Hutterer, 1994)													
M	5.86	11.80	-	-	-	5.79	-						
m	4.69	10.21	-	-	-	4.95	-						
X	5.21	10.82	-	-	-	5.28	-	0.48	-	-	-	-	4

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APPENDIX

Genital system comparison of the remaining *Canariella* subgenera

Subgenus *Canariella*: Other than the characters listed in the diagnosis of the genus, two of the epiphallar longitudinal folds extend in the penial cavity and merge in their distal end to form a spoon-like, grooved penial papilla. Distal portion of penis with longitudinal folds. Vagina with several digitiform vaginal glands.

Subgenus *Alvaradoa*: Penis without penial papilla and differentiated from the epiphallus only by a thickening of its longitudinal folds. Vagina with a large digitiform vaginal gland, simple or branched.

Subgenus *Simplicula*: Differentiation of penis and epiphallus indistinguishable. Penial papilla absent. Vagina with several non-digitiform vaginal glands, short and branched.

Tonnoidean gastropods of the North Atlantic Seamounts and the Azores

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Abstract: The benthos of the North Atlantic Seamounts around Great Meteor Bank contains an unusually high proportion of gastropods with teleplanic, planktotrophic larvae, including those belonging to the families Bursidae, Ranellidae, Personidae, and Cassidae. Some of the species have a very broad range in the Atlantic or are even world-wide in temperate and tropical waters, others seem to have a restricted range, being either apparently endemic to the seamounts or forming a local, isolated population there. The species that now have a restricted range are documented in the fossil record as formerly having a broader geographic distribution during the Pliocene, and it is suggested that the contemporary geographical restriction is due to narrow environmental requirements rather than to the lack of dispersal ability. Planktotrophic larval development appears to be one of the successful adaptations on the seamounts, a success that can be explained by the retention of larvae and by the low parental investment involved. Direct developers may be equally successful, but species with short-lived planktonic larvae are underrepresented.

The ranellid *Sassia lewisi* is recorded for the first time outside the Caribbean, the laubierinid *Akibumia orientalis* is newly recorded from the Atlantic Ocean, and the personid *Personopsis grasi* is recorded for the first time in the Recent fauna (Azores, Meteor Group seamounts, and Guadeloupe, West Indies).

Key Words: Ranellidae, Personidae, Laubierinidae, Bursidae, seamount, dispersal

Planktonic larval development in molluscs (Scheltema, 1971) is generally associated with the idea of a broad, in some species even cosmopolitan, geographic range. Many documented examples demonstrate that species with teleplanic larvae can cross the Atlantic within a single generation. Although this is generally verified, some of the species with teleplanic larvae may fail to become established in large areas and persist in geographic ranges that are similar to species of comparable size with direct development.

This paper examines species with planktotrophic development in the Superfamily Tonnoidea (Gastropoda) collected on the North Atlantic Seamounts and around the Azores. The "prosobranch" families Coralliophilidae and Fasciolariidae, and the heterobranch families Architectonicidae and Mathildidae also have planktotrophic larvae and are well represented on the Seamounts, but have been (Gofas, 2000) or will be studied elsewhere.

MATERIALS AND METHODS

The benthos around the Azores was sampled in 1971 by the Biaçores expedition, conducted under the direction of J. Forest (Muséum National d'Histoire Naturelle, Paris, hereafter MNHN). The Seamount expeditions were aimed at general collecting of the benthic fauna and a better understanding of the colonization of isolated sites by the benthic species. Seamount 1 was conducted in September/October 1987 by Philippe Bouchet (MNHN) and visited Gorringe, Josephine, Ampère, Lion, and Seine seamounts (57 dredge hauls and 10 beam trawl operations shallower than 1000 m). Seamount 2 was conducted in January/February 1993 by the first author and visited the Great Meteor Bank, Hyères, Irving, Plato, Atlantis, and Tyro seamounts (69 dredge hauls and 16 beam trawl operations shallower than 1000 m). The locations of the general collecting sites are shown in Fig. 1, and the details of localities from these cruises where tonnoideans were collected are given in Table 1. Further localities from other collections are given along with material examined, where relevant.

The material was sorted to the species level, and the provisional listing of molluscs for the depth interval shallower than 500 m records several thousand specimens representing 242 species in the Lusitanian seamounts, and 182 species in the Meteor group seamounts. Most of the specimens and species are in the size range of 1-5 mm. The largest part consisted of shells, and these were included in the mollusc counts. The material from Seamount 1 is shared between the Swedish Museum of Natural History, Stockholm, and MNHN; that of Biaçores and Seamount 2 is deposited in MNHN.

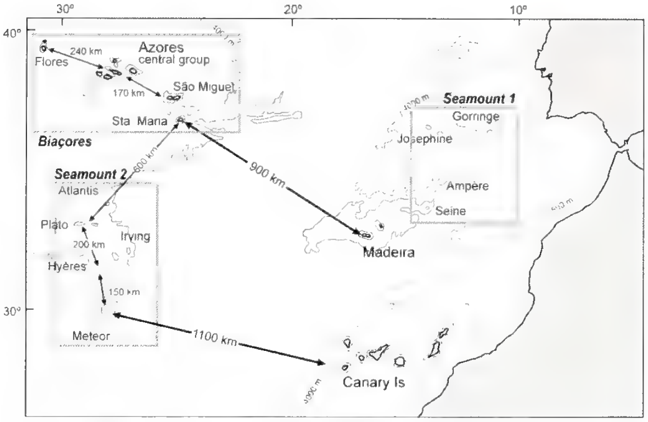

Fig. 1. Map showing locations of the Northeast Atlantic seamounts and their distances to the mainland.

The type of larval development is known for many of the species, but is mostly inferred from the morphology of the protoconch. A detailed statement of how protoconch morphology allows inference about larval development was given by Jablonski and Lutz (1980), the main point being the recognition of a well developed protoconch 2 following a distinct protoconch 1. In all illustrations, the dimensions of complete shells (given in mm) is the length, measured from apex to the tip of siphonal canal. The dimension of protoconchs is indicated by a scale bar. The abbreviations used for the material examined are: frg.: fragment, fragmentary. jv: juvenile. sh: shell(s). spm.: live-collected specimen(s). sta: station number of research vessel. IGNS: Institute of Geological and Nuclear Science, Lower Hutt, New Zealand. MNHN: Muséum National d'Histoire Naturelle, Paris, France (* denotes specimens stored in alcohol).

SYSTEMATICS

Family Ranellidae

Ranella olearia (Linné, 1758)
(Figs. 2, 3)

Material examined

Lusitanian seamounts, Gorringe bank, DW07: 2 (1 jv.) sh.. DE10: 4 (old) sh.. CP11: 1 (old) sh.. DW15: 3 frg. sh.. DW21: 1 frg. sh.; CP28: 1 spm. + 1 sh. Josephine bank, DW37: 2* spm. + 1 jv. sh.; DW41: 1 sh. (90 x 46 mm). DW43: 1 frg. sh.; DW61: 2 sh.. Seine bank, DE72: 1 frg. sh.; CP79: 6 spm. + 2 sh.. DW81: 1 frg. sh.; DE82: 1 sh.; Ampere bank, DE98: 1 jv. sh.; CP100: 2 (old) sh.

Meteor group seamounts, Meteor bank, CP144: 1 spm. (90 x 45.3 mm). CP146: 2 spm. (71.3 x 38 mm). DW172: 1 frg. sh.; Hyères bank, DW182: 1 spm. (65.1 x 34.3 mm) + 1 sh. (60.7 x 35.2 mm). DW188: 2 sh.; DW190: 1 spm. (64.8 x 34 mm) + 2 sh.. CP191: 1 sh. (57.8 x 31 mm). Irving bank, CP207: 2 spm.; DW209: 1 jv. spm. (11.6 x 7.7 mm); DW210: 2 sh.; Plato bank, DW240: 1 spm. (59 x 28 mm) + 4 sh. (45.1 x 27.2; 63.8 x 39 mm). DW246: 4 spm. (18.5 x 12.5; 59.2 x 32.2; 74 x 38.5; 76.7 x 38.8); Atlantis bank, DW254: 1 spm. (55.9 x 31.8 mm). DW255: 2* spm. (43 x 24.1. 71 x 34.5 mm); DW256: 1 sh.; CP257: 1 spm. (61 x 38 mm); DW258: 1 spm. (34 x 20.5 mm); DW274: 2 sh. (56.5 x 32.3. 62.4 x 36.5 mm).

Azores, "Biaçores" DG34: 1 sh. (47 x 27.5 mm). ChP41: 1 sh. (32.1 x 18.5 mm); DP79: 1 sh. (60 x 32 mm). DG88: 2 spm. (15.7 x 10; 41.5 x 22.2 mm); DP+F90: 1 spm. (63 x 35.5 mm); DG110: 1 spm. (34 x 19 mm) + 1 sh.; DR150: 1 spm. (32.1 x 18.5 mm); DP156: 1 sh. (33.5 x 19.5 mm); ChG161: 15 spm. (45.2 x 23.2 to 79.6 x 43.5 mm) + 3 sh.; DR166: 1 spm. (42.7 x 26 mm); DG168: 2 old sh. (50.5 x 33.9; 66.5 x 37.5 mm); ChG181: 1 spm. (28 x 22.5 mm) + 1 sh. (55 x 31 mm). ChG186: 3 spm. (34.8 x 20.5 to 51.7 x 31 mm); ChG239: 2 spm. (62.5 x 35.2; 75.2 x 42.5 mm) + 1 sh. (68.5 x 37.5); Monaco sta. 234, 39°01.3'N, 27°55.4'W, 454 m: 1 spm. (54.5 x 30.5) + 2 sh. (53.3 x 31. 61.8 x 33.8 mm).

Off western Brittany, "Procelt" sta. K224 (48°21.4'N, 10°11.5'W, 256-341 m, 6 spm. (128.5 x 62 to 151 x 84 mm); "Procelt" sta. K230 (48°08'N, 08°23'W, 368-454 m), 1 spm. (160 x 91 mm); Off Algarve, Portugal, from commercial trawler, 10 spm. (125 x 68 to 160 x 78 mm); Rabat, coll. Pallary, 1 spm. (173 x 86 mm); Alger, coll. Pallary, 1 spm. (210 x 97 mm); Cayar, Senegal, 100-200 m: 5 spm., leg. M. Pin (107.5 x 46.1 to 134.4 x 62 mm), all MNHN.

Guadeloupe, French West Indies, 1 sh., private collection of D. Lamy; Caribbean coast of Tobago, off Castare (120 m), 1 sh., American Museum of Natural History, 169202 and 1 sh., Academy of Natural Sciences of Philadelphia, 339436; Bermuda, off south shore (440 m), 2 sh., Delaware Museum of Natural History, 96988.

Remarks

This species is rather common around the Azores in 200-600 m (Fig. 3A, largest lot at 590 m) and well represented on the Meteor group seamounts on the upper part of the banks down to 750 m. However, the sizes of specimens in these populations is roughly half that observed in mainland populations (Fig. 3B).

The mainland range in the Eastern Atlantic spans from the SW British Islands to Angola. Records exist from the Caribbean, where it is rare: Colombia, off Guajira Peninsula (275-320 m), 3 sh. (Cosel, 1983); Southern Brazil to Uruguay, as "*Bursa barcellosi*," 6 sh. (Matthews *et al.*, 1973; Rios, 1994); off Castle Roads, SE Bermuda

Table 1. List of sampling stations of Seamount 1, Seamount 2, and Biaçores cruises where Tonnoideans were collected.

Gorringe bank			
DW07	36°28'N	11°34'W	350-355 m
DW09	36°31'N	11°38'W	350-360 m
DE10	36°27'N	11°35'W	500-545 m:
CP11	36°26'N	11°40'W	805-830 m:
DW15	36°33'N	11°29'W	300-330 m
DW21	36°35'N	11°28'W	460-480 m
CP28	36°38'N	11°30'W	605-675 m
Josephine bank			
DW37	36°42'N	14°18'W	255-270 m
DW38	36°41'N	14°17'W	235-245 m
CP40	36°39'N	14°16'W	215-221 m:
DW41	36°40'N	14°15'W	200 m
DW43	36°45'N	14°17'W	260-285 m
DW59	36°43'N	14°17'W	255-280 m
DW60	36°43'N	14°17'W	240-255 m
DW61	36°40'N	14°16'W	200-205 m
Seine bank			
DW68	33°45'N	14°23'W	180-185 m:
DW70	33°43'N	14°24'W	180-190 m:
DE72	33°45'N	14°21'W	165 m
DE73	33°45'N	14°24'W	165 m
DE75	33°47'N	14°21'W	181-194 m
DW76	33°47'N	14°23'W	175-180 m
DW78	33°49'N	14°23'W	235 m
CP79	33°49'N	14°23'W	242-260 m
DW81	33°49'N	14°23'W	270-310 m
DE82	33°48'N	14°24'W	320-400 m
Ampère bank			
DE95	35°05'N	12°55'W	197-210 m
DE98	35°03'N	12°55'W	300-325 m:
CP99	35°04'N	12°55'W	225-280 m
CP100	35°04'N	12°55'W	182-207 m
Meteor bank			
CP138	30°01.9'N	28°29.0'W	300 m
DE140	30°01.1'N	28°27.7'W	308 m
DW143	30°09.9'N	28°28.1'W	330 m
CP144	30°09.9'N	28°29.0'W	335 m
CP146	30°11.2'N	28°28.1'W	420 m
DW147	30°11.2'N	28°27.1'W	340 m
DW152	30°02.0'N	28°22.1'W	470 m
DW159	29°44.3'N	28°20.4'W	330 m
DW172	30°05.1'N	28°41.5'W	455 m
Hyères bank			
DW182	31°23.2'N	28°53.5'W	480 m
DW184	31°24.4'N	28°52.3'W	705 m
DW185	31°25.50'N	28°51.80'W	1250 m
DW188	31°30.0'N	28°59.5'W	310 m
DW190	31°29.0'N	29°00.0'W	750 m
CP191	31°30.2'N	28°58.9'W	295 m
DW200	31°19.1'N	28°36.0'W	1060 m
DW202	31°16.5'N	28°43.1'W	640 m
DW203	31°09.5'N	28°43.5'W	845 m

Table 1. Continued.

Irving bank			
DW205	32°01.1'N	27°57.2'W	348 m
DW206	31°59.8'N	28°00.0'W	260 m
CP207	31°59.7'N	28°00.4'W	260 m
DW208	32°03.90'N	27°53.9'W	790 m
DW209	31°59.2'N	27°55.9'W	460 m
DW210	32°02.6'N	27°56.7'W	320 m:
CP214	31°59.2'N	28°00.2'W	260 m
DW215	31°53.6'N	28°02.9'W	275 m
DW216	31°53.7'N	28°03.0'W	270 m
DW218	31°52.3'N	28°03.6'W:	480 m:
DW221	32°17.8'N	28°15.3'W	1180 m
CP224	32°12.2'N	28°15.4'W	1240 m
DW226	32°06.7'N	28°08.8'W	580 m:
Plato bank			
DW240	33°12.3'N	29°01.9'W	565 m
DW242	33°11.8'N	28°57.0'W	710 m
DW243	33°13.2'N	29°08.2'W	1420 m
DW244	33°12.1'N	29°11.9'W	1815 m
DW246	33°13.9'N-	29°36.1'W	520 m
DW248	33°13.6'N	29°32.5'W	735 m
DW250	33°12.6'N	29°17.2'W	1500 m
Atlantis bank			
DW254	34°05.3'N	30°13.4'W	280 m:
DW255	34°04.9'N	30°15.3'W	340 m
DW256	34°06.2'N	30°16.0'W	340 m
CP257	34°04.5'N	30°15.0'W	338 m:
DW258	33°59.8'N	30°12.1'W	420 m
DW261	34°22.4'N	30°27.8'W	1340 m
DW263	34°25.9'N	30°32.5'W	610 m
DW271	33°54.1'N	30°09.3'W	1220 m
DW274	34°05.1'N	30°13.6'W	280 m
Tyro bank			
DW 275	34°03.5'N	28°18.1'W	1665m
DW 276	34°02.1'N	28°19.0'W	1520m
Azores, "Biaçores" expedition			
DG34	38°09'N	29°15'W	650-670 m
ChP41	37°43'N	29°04'W	450-475 m:
DP79	39°00'N	27°54'W	360-380 m
DG88	39°02'N	28°06'W	400-450 m
DP+F90	39°04'N	28°07'W	205-210 m
DG110	39°33'N	31°17'W	300-350 m
DR150	37°37'N	25°35'W	550-600 m
DP156	37°37'N	25°54'W	350 m
ChG161	37°39'N	25°50'W	590 m
DR166	37°47'N	25°50'W	130 m
DG168	37°48'N	25°54'W	665-800 m
ChG181	37°53'N	25°35'W	450-620 m
ChG186	37°51'N	25°40'W	370-455 m
ChG195	37°56'N	24°49.5'W	1700-1776 m
ChG239	37°28'N	25°45'W	628-646 m

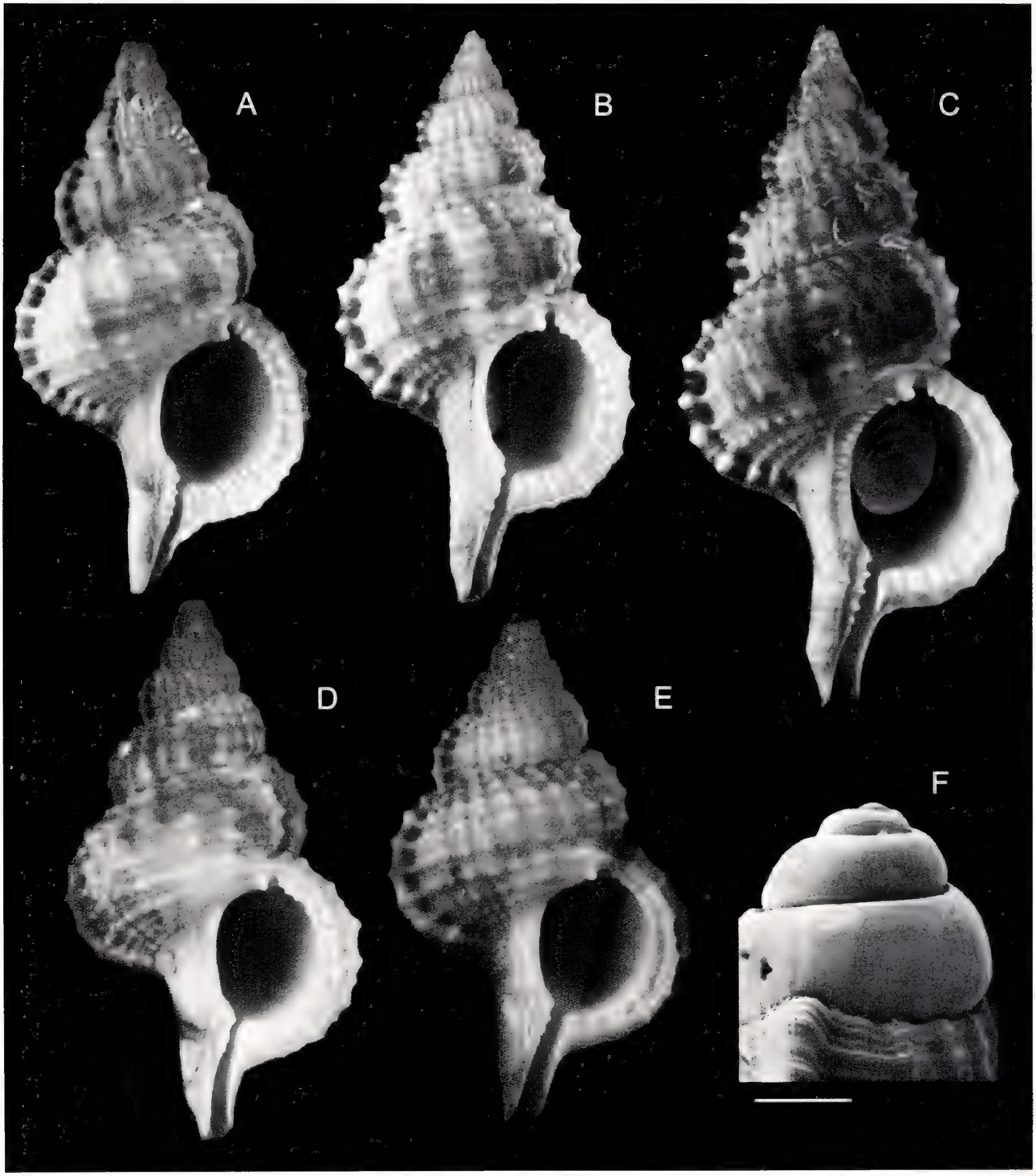

Fig. 2. *Ranella olearia* (Linné, 1758) from the North Atlantic seamounts and the Azores. A. Josephine bank, DW41 (length 90 mm). B. Meteor bank, CP144 (length 90 mm). C. Irving bank, CP207 (length 97 mm). D, E. Azores, "Biaçores" ChG161 (lengths 74.4 and 58.5 mm). F: Protoconch of a juvenile shell from Hyères bank, DW 188 (scale bar = 1 mm).

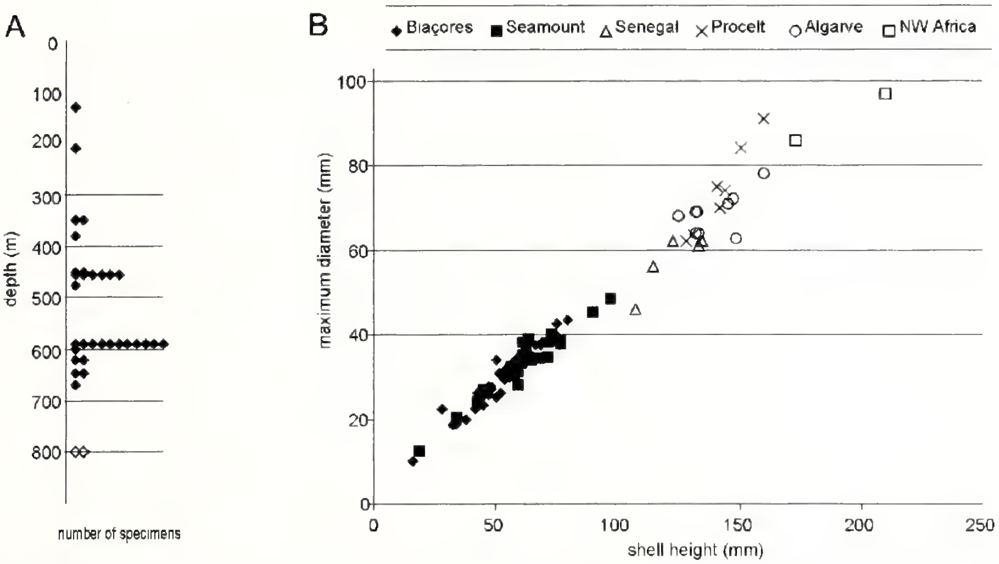

Fig. 3. A. Bathymetric distribution of *Ranella olearia* in the Azores and on the Meteor group seamounts. Each mark represents a specimen or shell; Hauls with less than 10 m difference in depth have been pooled. The 800 m haul (open diamonds) contained no living specimens. B. Plot of dimensions of *Ranella olearia* from the Azores (N = 53), the Meteor group seamounts (N = 25), Senegal (fosse de Cayar. N = 5), off Brittany ("Procelt" cruise. N = 7), off Algarve (N = 10) and NW Africa (N = 2). Specimens from Azores and seamount populations are roughly half the size of those from the mainland.

(220-260 m), "several" (Finlay and Vink, 1982) and museum material cited above. The species is also recorded from South Africa (Kilburn and Rippey, 1982: 76), the southern Indian Ocean (St. Paul and Amsterdam Islands; Arnaud and Beurois, 1972) and New Zealand (Dell and Dance, 1963; Powell, 1979) including the Chatham Islands (Beu, pers. obs.).

Charonia lampas (Linné, 1758)
(Figs. 4A-C)

Material examined

Lusitanian seamounts, Josephine bank, DW37: 1 sh.; DW38: 1 sh.; CP40: 1 sh.; DW41: 1 sh.; Seine bank, CP79: 3 sh. (160 x 72 mm); Ampere bank, CP100: 2 sh.

Azores, São Miguel, Ponta Delgada 10-20 m, 1 spm. (juvenile, 8.6 mm); Santa Maria, "Biaçores" dive P2 (15-18 m), 1 spm. (164 x 74 mm); "Biacores" dive P32, 1 spm. (83 x 43.5 mm); "Biaçores" dive P40, 1 spm. (138 x 63.5 mm); "São Pedro 1887," 1 spm. (118 x 61.5 mm).

Remarks

The forms found on the banks are relatively small for the species, slender and thin-shelled (as are offshore specimens throughout the range of the species). The current distribution in the Atlantic is mainly on the eastern continental margin, from the English Channel to Angola, and in the Western Mediterranean. Recent occurrences in the Western Atlantic are sparse (Bahia to Santa Catarina, Brazil. Rios, 1994). *Charonia lampas* also occurs in disjunct areas in the Indo-Pacific (South Africa; New Zealand and southern Australia; New Caledonia; southern Japan, Taiwan and, rarely, the Philippines; see Beu, 1998: 73).

Charonia variegata (Lamarck, 1816)
(Fig. 4D)

Material examined

Azores, Faial, Horta, "Biaçores" dive P8, 15 m: 1 sh. (190 x 79 mm).

Remarks

The two Atlantic species of *Charonia* are sympatric at the Azores, and also at Madeira and the Canaries (Nordsieck and García-Talavera, 1979). Specimens of *C. variegata* are much less common in shallow water around the Azores than is *C. lampas*, but empty shells are moderately common in fishermen's nets, and a few live-collected specimens have been seen in collections in the Azores (Gofas and Beu, pers. obs.).

Beu (1970) ranked *C. variegata* as a geographic subspecies of *C. tritonis* (Linné, 1758), the Indo-West Pacific form. However, Beu (1998) reached the conclusion that since the differences between these forms are marked and consistent, no intergradation occurs, and there is no possibility of larval exchange between these populations at present, they should be ranked as separate species. *Charonia variegata* differs from *C. tritonis* in reaching a much smaller maximum size, in its shorter spire, in its more

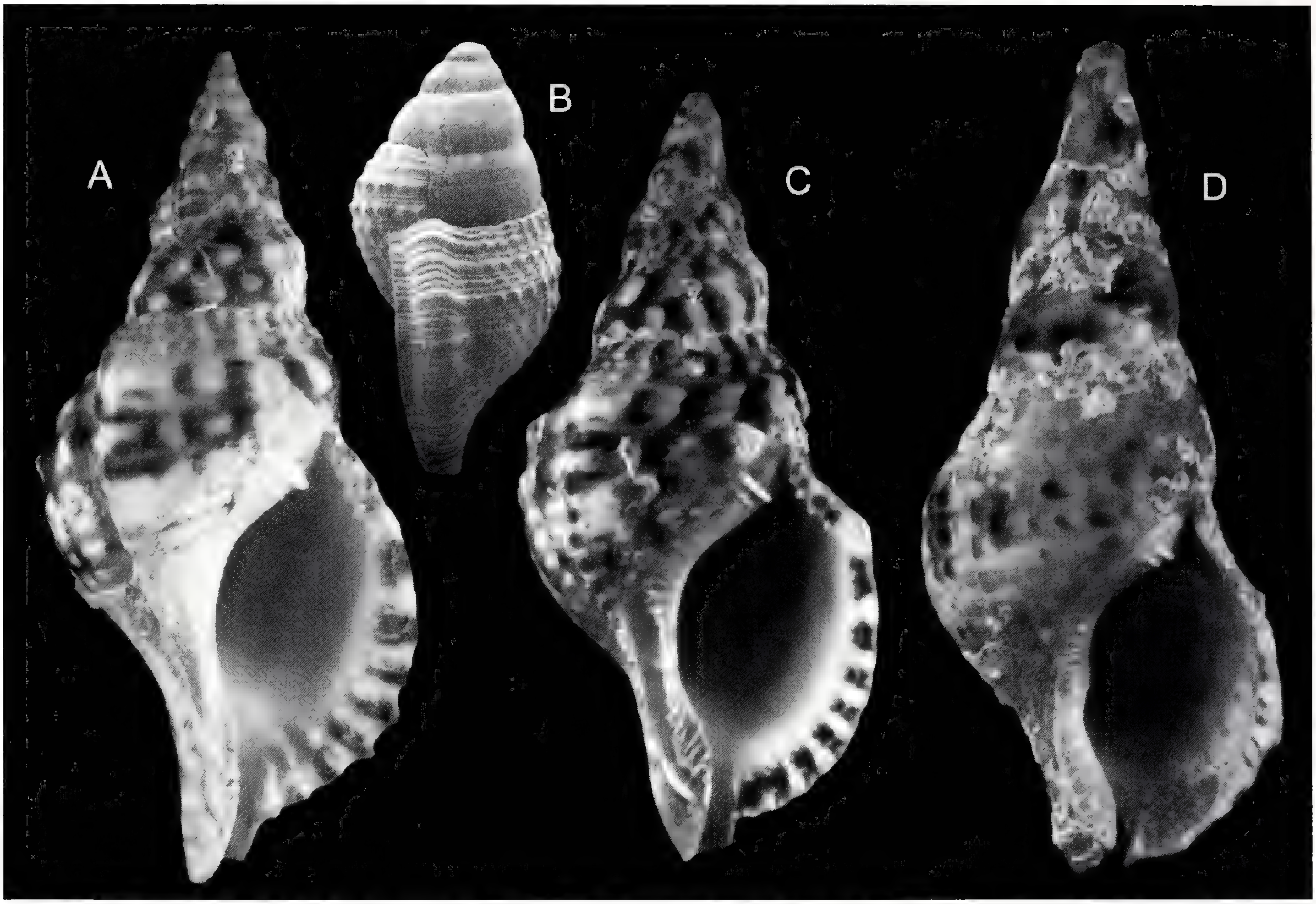

Fig. 4. *Charonia* spp. from the Lusitanian seamounts and the Azores. A. *Charonia lampas*, Seine bank, CP79 (length 160 mm). B. *C. lampas*, juvenile with preserved protoconch, São Miguel, Ponta Delgada 10-20 m (length 8.6 mm). C. *C. lampas*, Santa Maria, 15-18 m (length 164 mm). D. *C. variegata*, Faial, Horta 15 m (length 190 mm).

inflated and more strongly shouldered last whorl, in its more prominent nodules on the spiral cords, in its more constricted aperture with a less markedly flared outer lip, and in the much more obvious, darker, and more strongly ridged inner lip and interior of the outer lip. Typical *C. variegata*, as reported here, is common in the western Atlantic (Clench and Turner, 1957. Rios, 1994: North Carolina to Cabo Frio, Estado Rio de Janeiro, Brazil) but in the central and eastern Atlantic seems to occur only at St. Helena, Ascension, the Azores, the Canary Islands, and Madeira. A form usually identified as *C. variegata* occurs also in the Eastern Mediterranean, where it replaces *C. lampas*. The two overlap only in the Sicily straits (Russo *et al.*, 1990). The Mediterranean form has a taller, narrower, more weakly sculptured shell of duller, more purplish color than Atlantic specimens of *C. variegata*. It is conceivable that the Mediterranean form is a distinct species that has been isolated in the eastern Mediterranean since late Miocene time, and that the central and eastern Atlantic specimens of *C. variegata* represent pseudopopulations recruited from the western Atlantic. A genetic study still needs to be carried out to be sure that the two disjunct forms assigned to *C. variegata* are conspecific. The name *C. seguenzae* (Aradas and Benoit, 1870) is available for the Mediterranean form, should it prove distinct.

Cymatium parthenopeum (von Salis Marschlins, 1793)

Material examined

Azores, São Miguel, Ponta da Galera (20 m), 1 sh. (35.3 x 20.3 mm); Ponta da Galera (11 m): 2 sh. (58 x 29 mm. 60 x 34 mm); Ponta da Galera, “Biaçores” dive 29A (7-18 m): 1 sh. (52.3 x 26.5 mm); Faial, Baixa do Pesqueiro Longo (10-30 m): 2 old sh. (58 x 38 mm; 68 x 42 mm); Graciosa, Ilha da Praia (15 m): 1 spm. (64 mm), all MNHN; Santa Maria, beach at Praia, A. G. Beu, February 1998: 1 sh. (43.4 mm), IGNS.

Remarks

This widespread species is rather well represented in the Azores, and is also reported from Madeira and the

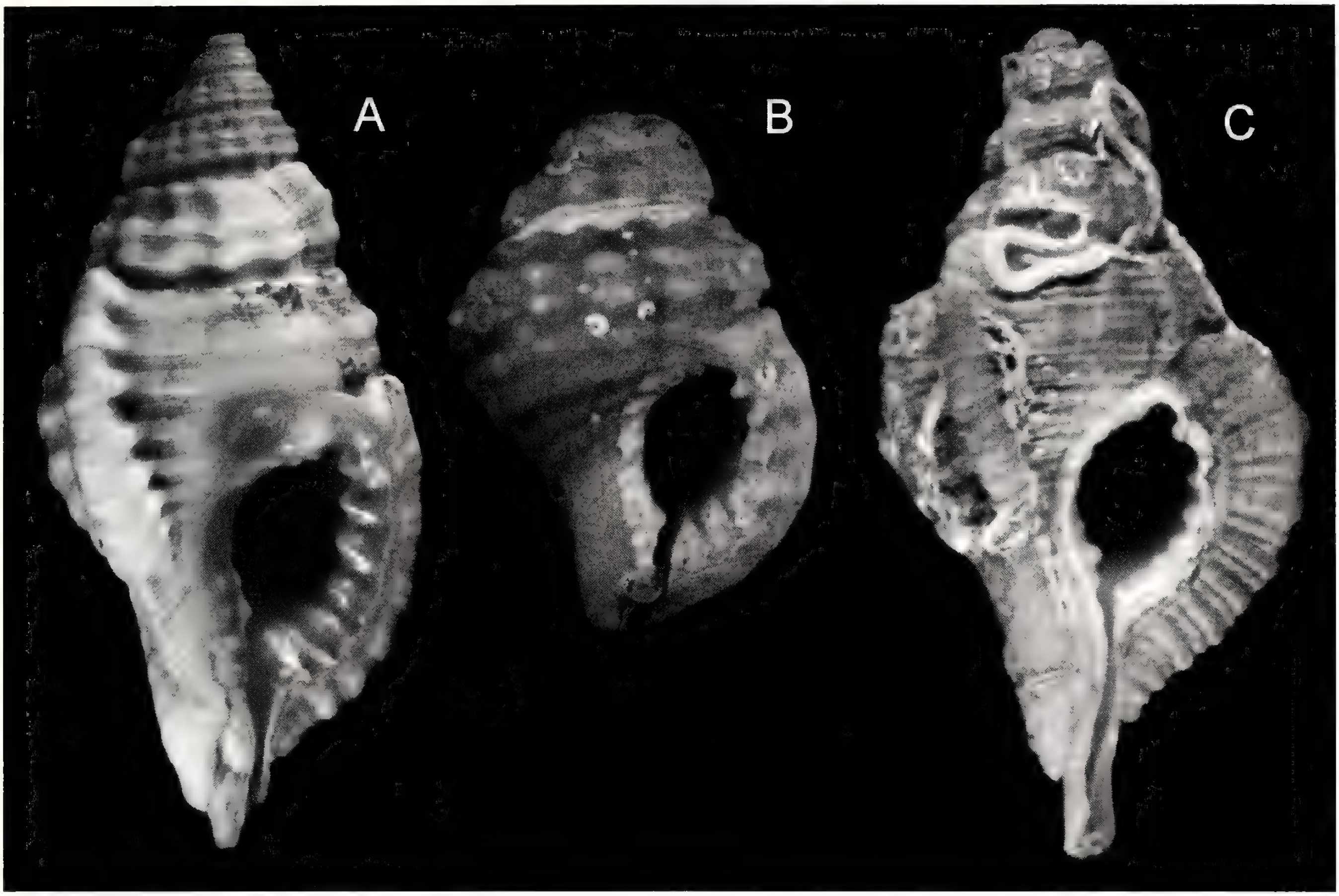

Fig. 5. Shallow water Ranellidae from Lusitanian seamounts and the Azores. A. *Cymatium corrugatum*, Seine bank, DW78 (length 45.9 mm). B. *Cymatium krebsii*, São Miguel, shore (length 23.3 mm). C. *Cymatium pharcidum*, Seine bank, DW70 (length 29 mm).

Canaries by Nordsieck and García-Talavera (1979). It is otherwise distributed in the Mediterranean and along both coasts of the Atlantic, from Portugal to Angola in the east and from North Carolina to northern Argentina in the west (Beu, pers. obs.).

Cymatium corrugatum (Lamarck, 1816)
(Fig. 5A)

Material examined

Lusitanian seamounts, Josephine bank, DW38: 2 frg. sh.; DW59: 1 frg. sh.; Seine bank, DE72: 1 sh.; DW78: 1 sh. (45.9 x 21.7 mm); Ampere bank, DE95: 1 frg. sh.

Cymatium krebsii (Mörch, 1877)
(Fig. 5B)

Material examined

Azores, São Miguel, Vila Franca do Campo, 1 sh. (23.3 x 15 mm); Santa Maria, beach at Praia, February 1998 (IGNS, WM15967, 2 fragments).

Remarks

The mainly Western Atlantic species *Cymatium krebsii* is very similar to the Eastern Atlantic *C. corrugatum*, the main differences being the much smaller maximum size of *C. krebsii*, and the color pattern with definite brown bands between spiral cords and no brown stain inside the aperture in *C. krebsii*, in contrast to the white exterior of *C. corrugatum* with a brown area inside the outer lip. Specimens of *C. krebsii* also have coarser sculpture and a more prominently lirate inner lip than in *C. corrugatum*, with two mid-columellar ridges more prominent than the others and more prominent than any in *C. corrugatum*. The more weakly lirate inner lip also is more deeply excavated in *C. corrugatum* than in *C. krebsii*, and the varices are markedly thicker and more prominent in *C. krebsii* than in *C. corrugatum*. We agree with García-Talavera (1987) that sympatric occurrence in the Canary Islands is a good argument for treating these as separate species, rather than treating *C. krebsii* as a subspecies of *C. corrugatum*. Judging by the prominent sculpture, bright exterior color pattern, and prominently sculptured, weakly

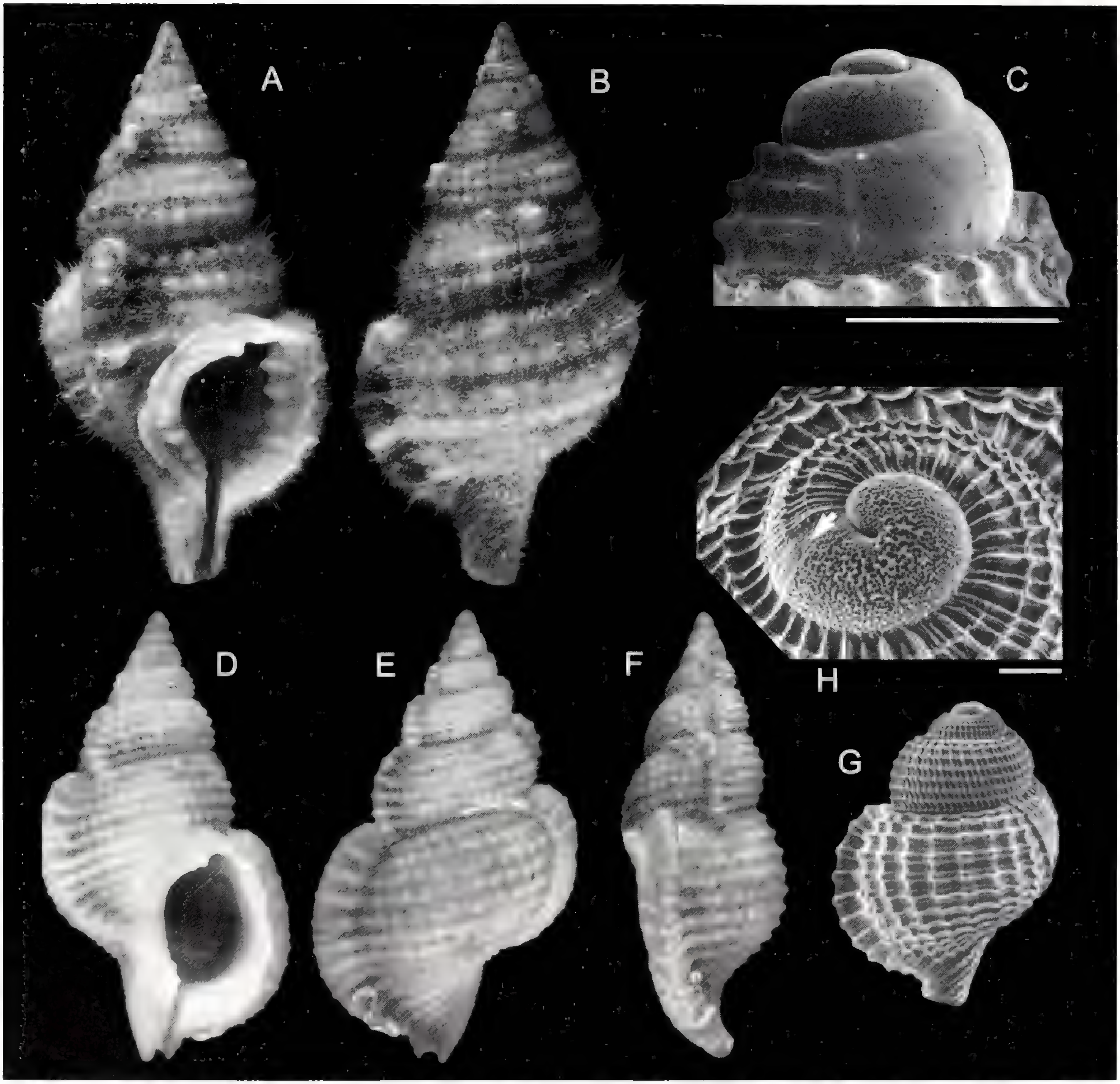

Fig. 6. Ranellidae from the Meteor group seamounts. A-B. *Sassia lewisi*, Meteor bank, CP144 (live collected specimen, length 38 mm). C. Protoconch of a juvenile shell from Hyères bank, DW188 (scale bar = 1 mm). D-F. *Halgyrineum louisae*, Irving bank, DW209 (length 26.2 mm). G-H. *H. louisae*, juvenile with larval shell, Atlantis bank, DW274 (length 2.7 mm), and detail of showing the limit (arrow) between protoconch 1 and protoconch 2 (scale bar = 100 µm).

excavated inner lip, we believe that the rather poor, incomplete material from the Azores belongs in *C. krebsii*.

Cymatium pharcidum (Dall, 1889)
(Fig. 5C)

Material examined

Lusitanian seamounts, Seine bank, DW70: 1 sh. (29 x 14.7 mm).

Remarks

There has been much confusion regarding the identity of this species, mainly because of a misidentification with *Cymatium krebsii* following Clench and Turner (1957). The first report of this species in the eastern Atlantic was from La Palma, Canary Islands, by Nordsieck and García-Talavera (1979) under the name *Cymatium tenuiliratum* (Lischke, 1873) (a closely related, larger

Indo-West Pacific species), and later under the correct name by García-Talavera (1987). It was reported alive from 100-150 m depth at Tenerife by Vega Luz and Vega-Luz (1995, as *Cymatium tenuiliratum*). The specimen collected on Seine Seamount is the third record from the Eastern Atlantic for this rare species.

Sassia lewisi Harasewych and Petuch, 1980
(Figs. 6A-C)

Material examined

Meteor group seamounts, Meteor bank, CP144: 1 spm. (38 x 20.2 mm); Hyères bank, DW188: 2 sh. (14.9 x 8.5 mm + 1 jv.); DW190: 2 spm. (18.1 x 9.8; 22.4 x 11.2 mm); Irving bank, DW209: 1 sh.; DW215: 1 sh.

Remarks

This is the first record of this species outside the Caribbean, and the first Recent record of the genus in the eastern Atlantic. The genus Sassia is represented in the European Pliocene by two other species, *Sassia apenninica* (Sassi, 1827) and *Sassia tuberculifera* (Bronn, 1831), neither of which is closely similar to the present species nor a likely ancestor to it. *Sassia lewisi* differs from *S. apenninica* in its sculpture of more numerous, more finely nodulous spiral cords, in its markedly wider anal sinus at the posterior end of the aperture, and in lacking prominent spiral and axial sculpture on the protoconch. The Meteor bank specimen is much the largest specimen of *S. lewisi* we have seen.

Halgyrineum louisae (Lewis, 1974)
(Figs. 6D-H)

Material examined

Meteor group seamounts, Meteor bank, CP138: 1 sh. (broken); Hyères bank, DW188: 1 sh. (11.0 x 7.0 mm); DW190: 1 sh. (18.5 x 11.8 mm); Irving bank, DW205: 1 sh.; DW209: 1 sh. (26.2 x 15 mm).

Remarks

Beu (1998) considered *Gyrineum atlanticum* Fechter, 1975, which has its type locality on Meteor bank, to be a synonym of *G. louisae*, and introduced for it the new genus *Halgyrineum*. The morphological similarity is convincing, and the possibility that the two populations, now totally lacking communication, are really conspecific is supported by the occurrence of two fossil lots in the Pleistocene of the Moín formation, Costa Rica (Robinson, 1990. Beu, 1998: 64).

In the Indo-Pacific, this is a rare species known only from the type locality, Hawaii, and three more occurrences in French Polynesia, on the Norfolk Ridge, New Caledonia, and at Réunion, with a depth range of 80-460 m (Beu, 1998). The material collected here is nearly as much as the total Indo-Pacific records. Recent specimens have not been recorded from the Caribbean, where, however, more intensive deep-water sampling is needed to be sure such species are absent. The protoconch of *H. louisae* is the plesiomorphic planktotrophic tonnoidean one, turbiniform with prominent spiral and axial sculpture, as in the *Sassia apenninica* species group and in species of *Bursa, Laubierina, Akibumia*, and *Oocorys* (Warén and Bouchet, 1990).

Family Laubierinidae

Pisanianura grimaldii (Dautzenberg, 1889)
(Fig. 7A)

Material examined

Meteor group seamounts, Meteor bank, DW152: 1 sh.; Hyères bank, DW185: 6 larval sh. and 1 frg.; DW200: 9 sh. (larval shells to small adults); DW203: 1 spm. and 11 sh. (larval shells and juveniles); Irving bank, DW221: 3 sh. Plato bank, DW243: 1 sh.; DW248: 1 frg.; DW250: 1 sh.). Atlantis bank, DW261: 3 frg.; DW263: 2 sh. (larval); DW271: 3 sh. Tyro bank, DW275: 1 spm. DW276: 2 spm. and 2 sh.) (total, 48 specimens, of which 4 were collected alive. live ones in 845-1665 m).

Remarks

Pisanianura grimaldii is moderately common in the Seamounts samples, and occurs alongside several specimens of *Laubierina* sp. (see below). Despite the relatively thick, coarsely sculptured adult teleoconch of *P. grimaldii* and the much thinner and more fragile, translucent teleoconch with several thin spiral keels in *Laubierina* sp., many of the more immature specimens are surprisingly difficult to distinguish at first sight. Their teleoconch spiral cords are similar in number and position, the teleoconch is white in both taxa, and the whorl profile and siphonal canals are closely similar in the two taxa. They can be distinguished by the protoconch, which is slightly smaller and pale yellow in *P. grimaldii*, whereas it is larger and red-brown in *Laubierina* sp., and contrasts strongly with the white teleoconch. Adult specimens also reach a larger size and become taller and narrower in *P. grimaldii* than in *Laubierina*. These slight differences seem to support a closer relationship between *Laubierina* and *Pisanianura* than was accepted by Warén and Bouchet (1990).

Laubierina sp.
(Fig. 7B-C)

Material examined

Meteor group seamounts, Hyères bank, DW185: 5

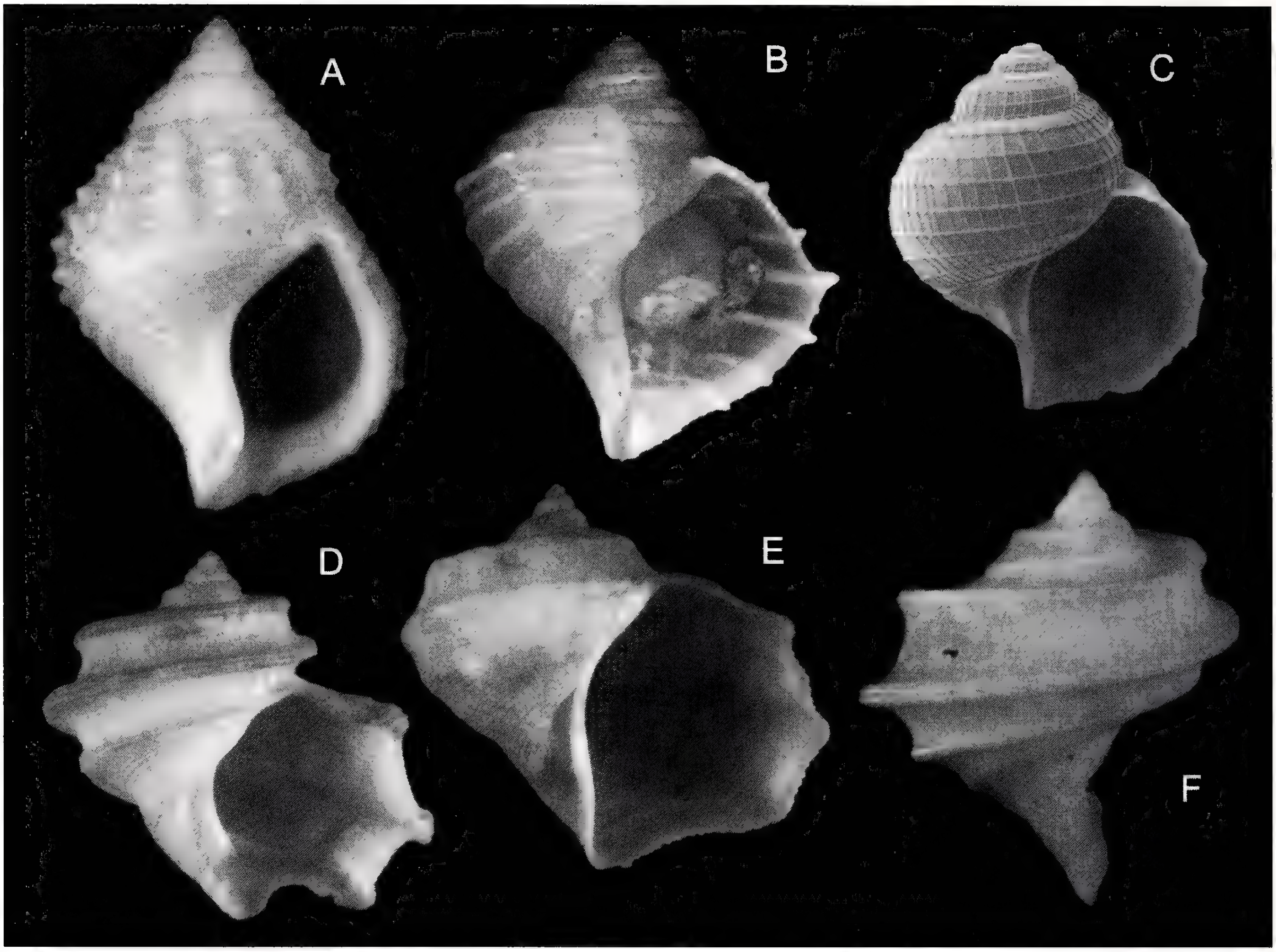

Fig. 7. Deep water tonnoideans from the Meteor group seamounts. A. *Pisanianura grimaldii*, Atlantis bank, DW271 (length 15 mm). B. *Laubierina* sp., Plato bank, DW244 (live collected specimen, length 8.9 mm). C. *Laubierina* sp., protoconch, Hyères bank, DW185 (length 4.8 mm). D-F. *Akibumia orientalis*, Plato bank, DW250 (lengths 13.5, 11.2, and 12 mm).

larval sh.; DW200: 1 sh. (protoconch only); Plato bank, DW242: 5 sh. (small, part-grown protoconchs, assigned tentatively); DW 244, 1* spm. (8.9 x 7.8 mm) and 1 spm. (protoconch + 0.8 teleoconch whorls); Tyro Bank, DW275: 1 spm. (protoconch + 0.1 teleoconch whorls); Madeira, R/V"Jean Charcot" 1969 sta. 13 (32°34'N, 17°07'W, 1970 m): 1 sh. (protoconch + 0.6 teleoconch whorls); Azores, "Biaçores" ChG195: 1 sh. (protoconch only).

Remarks

This is the species reported by Warén and Bouchet (1990) as *Laubierina* sp. A from the Azores and Madeira. The juvenile specimen from Plato bank is only 8.9 mm high, which is small compared to the 18.8 mm of the holotype of *L. peregrinatrix* Warén and Bouchet, 1990, type species of *Laubierina*, collected off Namibia. The sculpture has the same basic pattern with a peripheral keel and several prominent spiral cords, but the cords are much more prominent in the new species than in *L. peregrinatrix*. The species name, originally proposed as *peregrinator*, must be emended (to *peregrinatrix*, Latin, feminine of a traveler) under ICZN Code Article 31.2 (2000 ed.) to agree with the gender of the genus, which we presume to be feminine from the "*-ina*" suffix.

Akibumia orientalis (Schepman, 1909)
(Figs. 7D-F)

Material examined

Meteor group seamounts, Plato bank, DW250: 9 sh. (11.2 x 11.6 mm to 12 x 13.4 mm).

Remarks

This species has a conspicuous sculpture of three

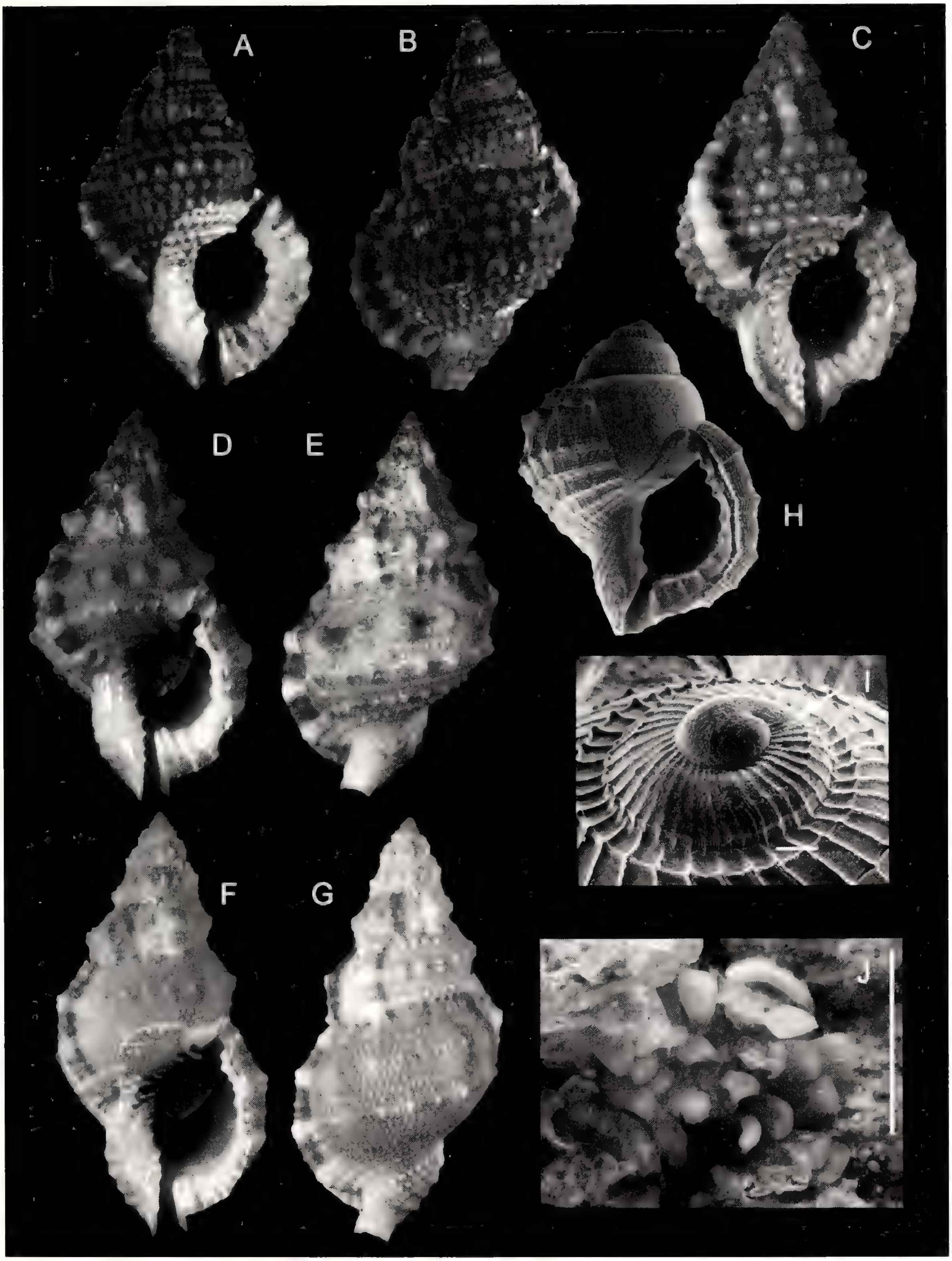

Fig. 8. *Bursa ranelloides* (Reeve, 1844) from the North Atlantic seamounts. A-B. Regularly beaded morph, Ampere bank, CP100 (length 45.3 mm). C. Ampère bank, CP99 (length 48.2 mm). D-E. Nodose morph, Irving bank, CP207 (length 40 mm). F-G. Finely sculptured morph *(tenuisculpta)*, Irving bank, CP214 (length 48.3 mm). H-I. Juvenile with larval shell, Meteor bank, DW159 (length 5.5 mm) and detail of apical part of larval shell, arrow showing limit of protoconch 1 (scale bar = 100 μm). J. Egg capsules from Irving CP214 collected with a living specimen (scale bar = 10 mm).

keels on the last teleoconch whorl and finer cords in between. There is much variation in the sculpture among the specimens collected, but the more prominent keels make a consistent difference from *Laubierina* sp. Moreover, the size of the protoconch, as can be extrapolated from the exposed part, is 2.5-3 mm, much smaller than the 4.5-5 mm in *Laubierina* species. We can see no significant difference between our specimens and the holotype from the Banda Sea (Warén and Bouchet, 1990: fig. 137) or specimens from Japan (Warén and Bouchet, 1990: figs. 136, 138). This is the first record for the Atlantic and implies a cosmopolitan distribution for the species.

Family Bursidae

Bursa ranelloides (Reeve, 1844)
(Fig. 8)

Material examined

Lusitanian seamounts, Gorringe bank, DW15: 1 old sh.; Josephine bank, DW37: 1 frg. sh.. DW60: 3 sh. (up to 66.1 x 36.8 mm); DW61: 1 sh.; Seine bank, DW68: 2 frg. sh.. DW70: 2 frg. sh.; DE72: 3 frg. sh.; DE73: 3 frg. sh.; DE75: 3 frg. sh.; DW76: 1 frg. sh.; CP79: 1 sh. + frg. sh.; Ampere bank, DE95: 1 frg. sh.; DE98: 1 frg. sh.; CP99: 3 sh. (up to 48.2 x 27 mm). CP100: 1 spm. (45.3 x 29.2mm).

Meteor group seamounts, Meteor bank, CP138: 1 frg. sh.; DE140: 1 frg. sh.; DW143: 3 frg. sh.; CP146: 1 sh. (34.1 x 19 mm); DW147: 1 juv. sh.; DW152: 2 spm. (32.1 x 18 to 40.5 x 22.3 mm) +juv. sh.; DW159: 1 spm. (48.7 x 27 mm) + 3 juv. sh.; DW172: 2 frg. sh.; Hyères bank, DW188: 1 sh. (41.8 x 24.3 mm) + 60 juv. sh.; DW190: 1 sh. (32.5 x17.8 mm) + 32 juv. sh.; CP191: 1 spm. (41.9 x 24 mm); Irving bank, DW205: 3 frg. sh.; DW206: 1 sh. (21 x 12.5 mm); CP207: 5 spm. (37.5 x 17.2 to 41.2 x 22 mm); DW209: 7 spm. (11.2 x 7.4 to 30.8 x 17.9 mm) + 6 sh.; DW210: 4 sh. (18.2 x 11.8 to 40.9 x 22.6 mm); CP 214: 15* spm. (29.8 x 17.5 to 48.3 x 24.5) + egg capsules*; DW215: 4 sh. (37.8 x 20.7 to 47.7 x 22.7 mm) + frg. sh.; DW216: 1 frg. sh.. DW217: 1 frg. sh.; DW218: 3 sh. (22.3 x 13.3 to 37.8 x 21.3 mm); DW226: 1 frg. sh.. Plato bank, DW246: 3 spm. (40 x 22.1 to 41.7 x 23.7 mm); Atlantis bank, DW254: 3 sh. (29.2 x 18.2 to 46.8 x 25.9 mm); DW255: 3* spm. (30.8 x 19 to 42.8 x 24.6 mm); DW256: 2 sh. (30 x 18.2 to 30.5 x 19 mm); CP257: 2 spm. (30 x 17.2 to 36.8 x 23 mm); DW258: 4 spm. (10.2 x 6.8 to 34.7 x 20 mm). Azores, "Biaçores", DG110: 1 sh. (39.5 x 24 mm).

Remarks

Bursa ranelloides is one of the common species on the banks, and was reported from Seine bank by Dautzenberg and Fischer (1906). The variation in sculpture is important, and this supports the view expressed by Beu (1998: 161) that it cannot be used to separate the two subspecies *ranelloides* and *tenuisculpta*. The beaded form (Fig. 8A-C) is prevalent in the Lusitanian seamounts, but also occurs in the Meteor group. The *tenuisculpta* form (Fig. 8F-G) was only found in the Meteor group, and there are also specimens with fine sculpture but some very prominent rows of knobs on the penultimate and last whorls (Figs. 8D-E). Specimens in a particular lot tend to be homogeneous for shell morphology. In CP214, the 15 specimens collected alive are *tenuisculpta* but two (older) shells found in the same haul were beaded forms. The particular morphology found in one place may depend on the origin of the particular batch of larvae by which recruitment was achieved.

The general distribution of the species is widespread, in the Indo-West Pacific in southern Japan (Beu, 1998: 161) to Taiwan and perhaps the Philippines, in the Indian Ocean, and in the Atlantic in the Caribbean (e. g, Abbott, 1974: 166, fig. 1778; Beu, pers. obs.), the Azores and Madeira (Dautzenberg and Fischer, 1906), and the Canaries (Nordsieck and García-Talavera, 1979; Vega Luz and Vega Luz, 1996) but not West Africa.

Bursa scrobilator (Linné, 1758)

Material examined

Azores, "Santa Clara 19.9.1887," 1 spm. in MNHN (54.4 mm); Santa Maria, beach at Praia, A. G. Beu, February 1998: 1 sh. (28.9 mm), IGNS.

Remarks

This species is stated to be present in the Azores, Madeira, and Canaries by Nordsieck and García Talavera (1979) and recorded as rare in the Canaries by Vega Luz and Vega Luz (1995). It is a shallow-water species, occurring also in the Mediterranean and the Ibero-Moroccan area. A similar form is found along the West African coast as far south as Angola (see Verdejo Guirao, 2001, for distribution).

Bufonaria marginata (Gmelin, 1791)

Material examined

Lusitanian seamounts, Seine bank, DW78: 1 jv. sh.

Remarks

A single juvenile specimen was found on the banks of this common West African species, which is also known from the Canary Islands (Odhner, 1932: 16-17; Nordsieck and García-Talavera, 1979, and our material from Gran Canaria), but not from Morocco nor from the Mediterranean. The Mediterranean record by Di Natale (1982) is best explained as a specimen accidentally cast

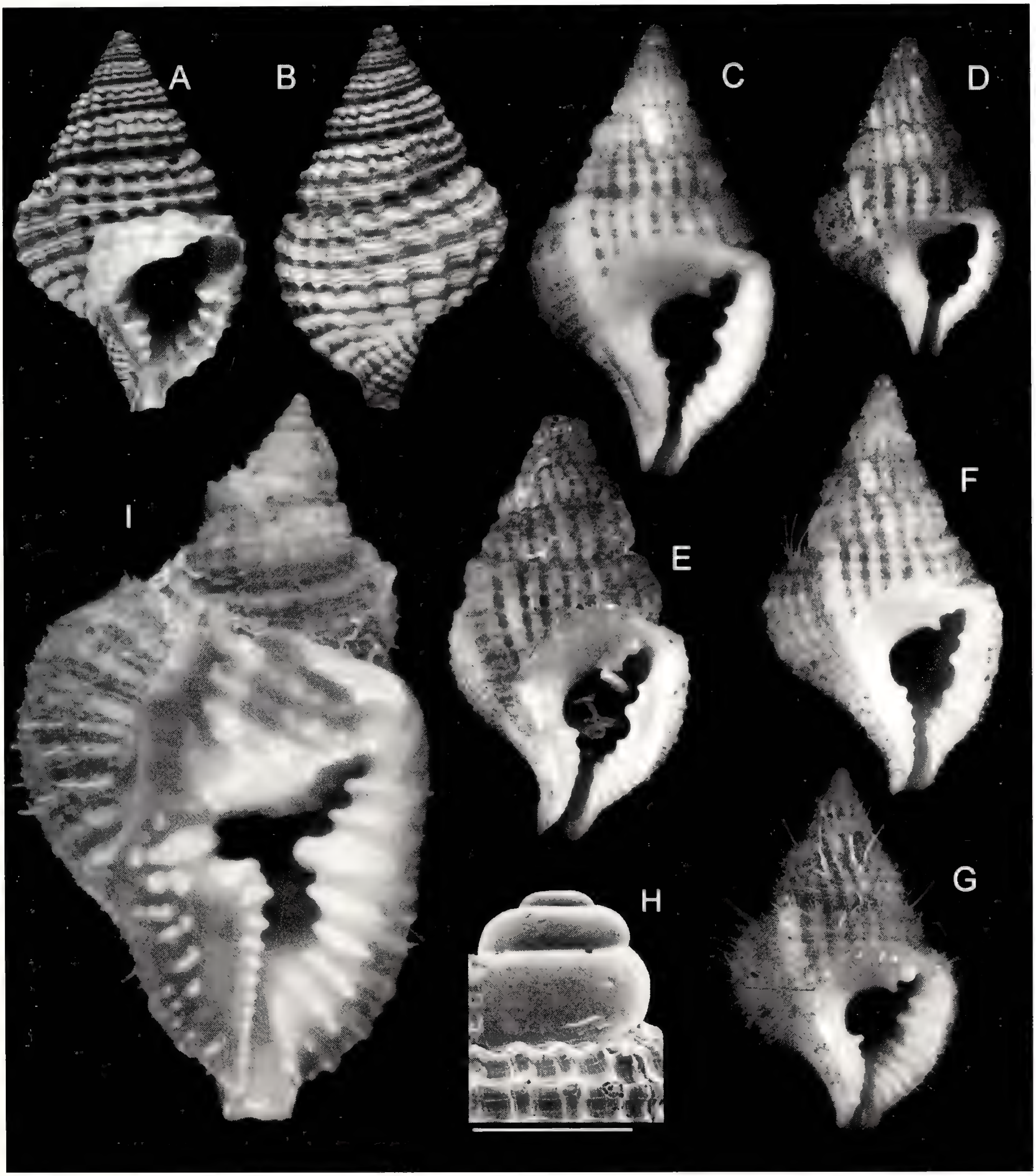

Fig. 9. Personidae from the Italian Pliocene and from North Atlantic seamounts. A-B. *Personopsis grasi*, Pliocene fossil, Liguria, Italy (length 22.5 mm). C. *P. grasi*, Azores, "Biaçores" DG110 (length 24.6 mm). D. Atlantis bank, DW254 (length 12.3 mm). E. Irving bank, DW215 (length 23.5 mm). F. Hyères bank, CP191 (length 20 mm). G. Plato bank, DW 248 (length 23.5 mm). H. Protoconch, same specimen as D. I. *Distorsio perdistorta*, Seine bank, CP79 (length 70 mm).

overboard by a fishing boat operating in West Africa, and we are reluctant to accept the general statement (without reference to a particular material) of its occurrence in Morocco by Vega Luz and Vega Luz (1995).

Family Personidae

Distorsio perdistorta Fulton, 1938
(Fig. 9I)

Material examined

Lusitanian seamounts, Seine bank, CP79: 1* spm. (70 x 40 mm).

Remarks

The more common *Distorsio* species along the West African coast is *D. smithi* (von Maltzan, 1887), a continental shelf species which grows to a larger size (110 mm) and is considerably more coarsely sculptured than *D. perdistorta*. Its wide, flat zone between the two peripheral rows of nodules contrasts strongly with the evenly convex whorls of *D. perdistorta. Distorsio perdistorta* has been found only rarely in the Atlantic, and was not recognized there until Lewis (1972) recorded specimens from the Gulf of Mexico; off Tampa Bay, Florida, USA. Several specimens are now known from deep shelf sites in the western Atlantic. Nordsieck and García-Talavera (1979) recorded a specimen from off the Canary Islands, and Beu (1998: 195) recorded a specimen from the Gulf of Guinea, in 100 m. More recently, Kronenberg (1999) recorded three specimens collected by fishermen in 110 m off Ambriz, Angola. This therefore seems to be an uncommon species occurring throughout the Indo-West Pacific and eastern and western Atlantic Oceans. In the eastern Atlantic it seems to live slightly deeper than the range of *D. smithi*.

Personopsis grasi (Bellardi in d'Ancona, 1873)
(Figs. 9A-H)

Material examined

Meteor group seamounts, Hyères bank, DW188: 1 sh.; CP191: 1 spm. (20 x 11.4 mm); Irving bank, DW209: 1 sh.; DW215: 1 sh. (23.5 x 13.2 mm). DW218: 1 sh.; Plato bank, DW248: 1* spm. (23.5 x 14.7 mm); Atlantis bank, DW254: 1 sh. (12.3 x 7.44 mm); Azores, "Biaçores" DG110: 1 sh. (24.6 x 13.4 mm).

Guadeloupe, French West Indies, off Basse Terre (in fishermen's traps, 300 m), collected by D. Lamy, January 2001 (5 sh. – IGNS, WM 17192, 2 sh.; 3 sh. in private collection of D. Lamy).

Italy – Zinola, Liguria, Pliocene fossil, 1 sh. (Staadt collection, MNHN. 22.5 x 13.6 mm); Savona, 1 sh. (H. 17139) and Bacedasco, near Piacenza, 1 sh. (H. 17140), both in Mayer-Eymar collection, Naturhistorisches Museum Basel (Beu, 1998: fig. 67 1-k).

Remarks

The records above are the only ones of *Personopsis grasi* among Recent material, and of the genus living in the Atlantic. The only morphological differences between the fossil specimens examined and the Seamount 2 and Guadeloupe specimens is in size (the Pliocene fossils are rather larger than the Recent specimens) and the slightly coarser sculpture of the fossils. The variation in shape and sculpture among the Recent specimens is large, and the fossils show a similar range of variation in spire height and aperture shape. We judge them to be conspecific, although it is desirable to examine additional fossils to evaluate the sculptural difference. *Personopsis purpurata* Beu, 1998 and *P. trigonaperta* Beu, 1998 are similar Indo-Pacific species. The former is distinguished by its still smaller size (16-18 mm), its finer sculpture, and a purple blotch on the anterior part of the canal, the latter by having a much longer canal, which is parallel to the coiling axis and not deviating as in *P. grasi*.

Family Cassidae

Semicassis saburon (Bruguière, 1792)
(Fig. 10F)

Material examined

Lusitanian seamounts, Gorringe bank, DE10: 1 sh.; Josephine bank, DW37: 1 frg. sh.. DW38: 1 frg. sh.; DW41: 3 frg. sh. (45.7 mm and 32 mm). DW43: 1 sh.; Seine bank, CP79: 1 frg. sh.

Semicassis undulata (Gmelin, 1971)

Material examined

Lusitanian seamounts, Gorringe bank, DW09: 1 frg. sh. (20 mm wide).

Oocorys sulcata Fischer, 1883
(Fig. 10A-B)

Material examined

Azores – We examined a large amount of material from the "Biaçores" expedition, cited by Bouchet and Warén (1993).

Remarks

This species was not found on the seamounts, possibly because very few hauls were taken in the normal depth range of this species, around 2000 m.

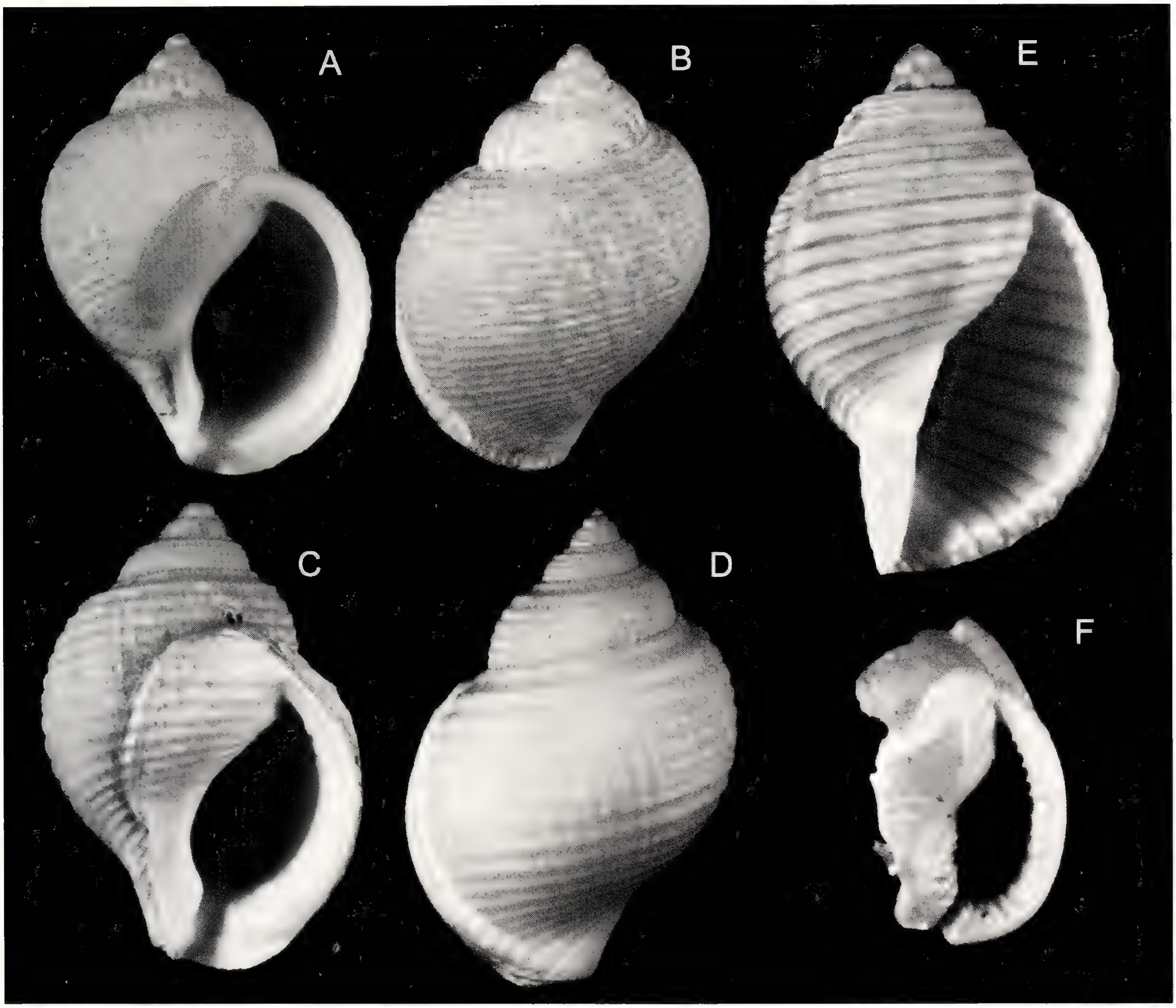

Fig. 10. Cassidae and Tonnidae from the Azores and the North Atlantic seamounts. A-B. *Oocorys sulcata*, Azores, Biaçores ChG176 (length 25.4 mm). C-D. *Oocorys verrilii*, Irving bank, CP 224 (length 32.1 mm). E. *Eudolium bairdii*, Hyères DW184 (length 29.2 mm). F. *Semicassis saburon*, Josephine bank, DW41 (length 45.7 mm).

Oocorys verrillii (Dall, 1889)
(Fig. 10C-D)

Material examined

Meteor group seamounts, Irving bank, CP224: 3 old shells (32.1 x 21.1 mm).

Remarks

This species differs from *Oocorys sulcata* in having distinctly cancellate teleoconch sculpture. This species was reported from the Azores under the name *O. cancellata* Dautzenberg and Fischer, 1897 by Bouchet and Warén (1993), and its revised name used here will be discussed by Beu and Bouchet (in prep). It was represented in the Seamount material only by these three old shells, encrusted with black oxide deposits. Probably, then, these are long-dead, fossil specimens representing an earlier pseudopopulation. We concur with Bouchet and Warén that this species cannot be considered as represented in the Recent Eastern Atlantic fauna.

Family Tonnidae

Eudolium bairdii (Verrill and Smith, 1881)
(Fig. 10E)

Material examined

Meteor group seamounts, Hyères bank, DW184: 1 spm. + 1 juv. (29.2 x 19.1 mm). DW 202, 3 frg. sh.; DW208, 1 sh.; DW226, 1 frg. sh.

Azores, "Biaçores" GhG161: 1 juv. spm. (figured by Warén and Bouchet, 1990, figs. 78-79, as *Eudolium crosseanum*).

DISCUSSION

Ability to disperse, geographic and bathymetric range

In all the species of tonnoideans found in North Atlantic oceanic locations, the morphology of larval shells indicates they are planktotrophic species with teleplanic larvae. Thus, all the species might be expected to have broad geographic ranges (Scheltema, 1971) so as to occur also along the European and/or American mainland. In contrast to this, what we actually found is a clear bathymetric stratification of the species in three scarcely overlapping groups.

The first group of species includes those ranging from shallow subtidal depths to ca. 200 m: *Charonia* spp., *Cymatium* spp., *Semicassis* spp., *Bursa scrobilator*. These are the typical "tramp species," which may settle and grow in remote locations with or without establishing perennial populations there. In our material, *Charonia lampas* and *Cymatium parthenopeum* are rather well represented in the Azores and probably reproduce there, but it is likely that the specimens in this category found on the Lusitanian seamounts represent pseudopopulations. The species collected on the Lusitanian seamounts occur there in deeper water than along the mainland, where they are normally shelf species and occur in less than 200 m. This reflects a "depressed" character of the seamount faunas: because of the low diversity, deep-sea species from the surrounding slope occur in shallower water on the seamounts than they do on the mainland shelf, and conversely the few shelf species that reach the seamounts may occur in deeper water than they do on the mainland shelf.

A second category includes species that are best represented in the 300-600 m depth interval and may be considered a genuine component of a "seamount fauna" (that of the upper part of the seamounts) in the Meteor group. This includes *Ranella olearia*, which is also common on the mainland outer shelf and slope, but also several species that are rare (e. g. *Sassia lewisi, Bursa ranelloides*) or unrecorded (e. g. *Halgyrineum louisae, Personopsis grasi*) in the corresponding interval of the mainland slope. There is no obvious external source area for a continuous influx of larvae, and we conclude that the populations of the seamounts are self-sustaining. Egg capsules were recorded for *Bursa ranelloides*.

In the case of species with teleplanic larvae, ecological factors other than distance may limit geographical distribution. A major characteristic of the physical environment on the Seamounts is the lack of any terrigenous input of fine sediments, as occurs on continental margins. The only source of new sediment, apart from the erosion of the geological structure itself, is the production of bioclasts by pelagic and benthic organisms. This is a slow process, and allows time for winnowing away most of the fine particles. The winnowing and the rugged topography also lead to the availability of large rock surfaces in the 200-600 m depth interval, which is usually clad with sediments along the continental margin. Exposed deep rock is likely to be the environment inhabited by *Personopsis grasi* also around Guadeloupe, West Indies. The fossil record indicates that some of the species involved here had a former range in the Atlantic that included the European or American mainland, in sites that apparently did not agree with the sedimentological setting of the seamounts. These species may have restricted or shifted their substrate needs since Pliocene time, or alternatively, conditions on the mainland slope may have changed, with an increase of muddy sedimentation. Here there is an ecological constraint determining the distribution of Holocene forms. A third group is constituted by bathyal species, found in depths of 600 m or greater. These include *Pisanianura grimaldii, Laubierina* sp. and *Akibumia orientalis*, which are considered to be cosmopolitan at the appropriate depth interval, and the *Oocorys* and *Eudolium* species which may be equally widespread. Since this depth interval was not the main target of the Seamount cruises, the sampling effort there was not intense. The available area for these species is considerably larger than the seamount habitat, and continues indefinitely stepwise northwards and southwards along the Mid Atlantic Ridge. The area in a depth range of 600-2000 m between Meteor Bank and the Azores is of approximately 250,000 km^2, several hundred times the total surface of the Meteor group seamount tops shallower than 600 m. Thus, species in this third group are neither insular nor isolated, but part of a vast bathyal continuum in the Atlantic.

Disjunct populations and the antiquity of Tonnoidean species

The decision to treat forms originating from remote, widely separated populations as a single species depends on the following assumptions: larval dispersal throughout the world ocean can be achieved, to keep the disjunct adults in genetic continuity, and/or the evolutionary origin of the species predates the final separation of the Eastern Pacific and Western Atlantic. The separation in the tropical realm by the uplift of the isthmus of Panama is thought to have occurred 3.5 million years ago (Coates *et al.*, 1992), although marine connections may have continued in periods of high sea-level during late Pliocene-early Pleistocene time (Beu, 2001). The hypothesis regarding allopatric populations as representing a single species (as in *Halgyrineum louisae*) or as separate biological species (as in *Charonia variegata* and *Charonia tritonis*) relies on the amount of recognizable morphological difference (that is not ecophenotypic). Thus, we are aware that it is an arbitrary decision based on how consistently differences can be diagnosed, and on scaling the morphological differences between allopatric populations to those observed between sympatric biological species in the same taxonomic group.

Halgyrineum louisae has two disjunct ranges, one in the Indo-Pacific, the other in the central North Atlantic. In this case the decision to treat them as conspecific assumes that the species is at least Pliocene in age and that the Recent representatives are conspecific with the Central American fossils. A similar assumption of a Pliocene age is made for *Personopsis grasi*, which has its type locality in the Italian Pliocene and is now extinct in European seas.

Conversely, many of the species considered here were described as Recent but have a fossil record that can be traced back to the Pliocene and Miocene: *Ranella olearia, Cymatium corrugatum, Cymatium parthenopeum, Charonia lampas* and *C. variegata*, *Bufonaria marginata*, *Bursa scrobilator* (Bellardi, 1873; Magne and Vergneau-Saubade, 1973, on *Charonia*). Thus we assume species durations of more than 5 million years (and, in some cases, more than 20 m. y.), but this is consistent with what is known for eurytopic molluscan species with planktotrophic development (Jablonski and Lutz, 1980; see also Central American tonnoidean species listed by Beu, 2001).

The case for present-day circumglobal dispersal is tenable for the deep water species, such as *Oocorys sulcata, O. verrillii, Eudolium bairdii, Pisanianura grimaldii, Akibumia orientalis,* and *Laubierina* sp. Other, shallower-living species with widespread but strongly disjunct populations (such as *Ranella olearia, Charonia lampas,* and *Cymatium parthenopeum*) have more limited ranges as adults. *Ranella olearia* apparently is carried as larvae from South Africa to St. Paul and Amsterdam Islands and New Zealand (but, strangely, in this case not to Australia) but has no other Indo-West Pacific records. A similar mechanism possibly explains Australasian occurrences of *Charonia lampas*. However, this latter species could also have entered the Indo-West Pacific via the Arabian Gulf from Europe before the Middle Miocene closure of the Paratethys seaway (Rögl, 1998), which would explain its occurrence now around Japan and Middle and Late Miocene occurrences in Australia and New Zealand. Other ranellids such as *Fusitriton magellanicus* (Röding, 1798) and *Argobuccinum pustulosum* (Lightfoot, 1786) are also apparently transported as planktotrophic larvae around the Southern Ocean by the Antarctic Circumpolar Current, maintaining the benthic adult populations in genetic continuity. The case of *Cymatium parthenopeum* is more complex, as this species (and very closely similar forms such as the Panamic species *C. keenae* Beu, 1970) inhabits much of the temperate and tropical fringe of the world ocean, except that it is rare or absent from most of the central tropical Indo-West Pacific. Here it seems likely that an originally cosmopolitan distribution (during Miocene-Pliocene time?) has been disrupted through unsuccessful competition with the very similar Indo-West Pacific species *C. pileare* (Linné, 1758). This is the only shallow-water tonnoidean that probably originally had a cosmopolitan distribution in temperate and tropical seas.

The success of the planktotrophic mode on the seamounts

Semi-quantitative data on the Seamount fauna suggest that planktotrophic, teleplanic larval development is one of the successful modes there, the other being direct development. The tonnoideans, which have the greatest expression of the planktotrophic mode of development, are conspicuous in the benthic community on seamounts, and appear overrepresented when compared to mainland faunas. In the coarse size fraction (<10 mm) of the seamount fauna collected above 600 m in the Meteor group, the ranellid and bursid species considered herein make up some 150 specimens or shells, roughly one quarter of the total catch of molluscs in this size range. The remaining large molluscs are mostly the Fasciolariidae, Muricidae, and Coralliophilidae, of which only two species are non-planktotrophic (Houart, 1996; Gofas, 2000). Large molluscs with planktotrophic development but short-to medium larval life spans (e. g. Cypraeidae, Naticidae, Nassariidae, most bivalves) are conspicuously underrepresented. As a point of comparison, in a large sampling effort on the southwest Iberian coast (Mission Algarve) carried out by MNHN in May 1988, tonnoideans represent less than 1% of specimens in the total catch in the same size fraction.

The production of planktotrophic larvae in the seamount context possibly implies a waste of reproductive effort for species with teleplanic larvae, but this waste is evidently sustainable. First, the larvae are very small at the time of hatching (as shown by the small size of protoconch 1), and the bulk of the investment in larval growth is not made by the parent. Second, the fact that these species have persisted demonstrates that retention around the seamounts (see Scheltema *et al.*, 1996; Mullineaux and Mills, 1997) is sufficient to ensure recruitment. Third, the species shared with the mainland at least can also export larvae that will grow in remote areas and will contribute to later generations.

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Changes in the freshwater mussel communities of Lake Pepin, Upper Mississippi River, Minnesota and Wisconsin, 1990-1997

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Abstract: Densities of unionid mussels were measured at 7 mussel beds in Lake Pepin, Upper Mississippi River Mile (MRM) 784.2 - 764.5, Minnesota and Wisconsin, from 1990 to 1997. Densities of the commercially harvested threeridge, *Amblema plicata*, declined at 5 of the 7 mussel beds sampled. The most dramatic decline occurred at the Hok Si La, Minnesota, mussel bed where densities of *A. plicata* averaged about 22 mussels/m^2 in 1993, and declined to ≤6/m^2 between 1995-97 (F=14.940, df=4, P<0.0001). Densities of non-harvested mussel species remained constant at all but one bed during this research project. Shell height distributions for *A. plicata* indicate that there is little or no recent recruitment evident for this species within the sampled mussel beds of Lake Pepin. During this study, zebra mussels *(Dreissena polymorpha)* became established in Lake Pepin. The greatest density of *D. polymorpha* was found in the downstream portion of the lake, where they had been steadily increasing, reaching average densities of over 4,000 mussels/m^2 in 1997. Our results suggest that commercial harvest of *A. plicata* is having a negative impact upon their populations within Lake Pepin. We suggest that the findings of the present study, along with population estimates of *A. plicata* and *D. polymorpha*, be incorporated into management recommendations that will ensure the continued survival of *A. plicata* populations into the future.

Key Words: Unionidae, Dreissenidae, harvest

Lake Pepin, a 40 km long natural widening of the upper Mississippi River between Minnesota and Wisconsin, historically harbored a diverse freshwater mussel assemblage (Wilson and Danglade, 1914; Grier, 1922; Grier and Mueller, 1922; Southall, 1925; Ellis, 1931). A decline in unionid population densities in Lake Pepin began in the early 1900s and has been attributed to commercial harvest, water pollution originating from the Twin Cities, Minnesota, and habitat degradation (Grier, 1922; Southall, 1925; Ellis, 1931; Fuller, 1978; Thiel, 1981).

Because some mussel species residing in Lake Pepin are commercially valuable, and therefore harvested for the cultured pearl industry, there is concern that over-harvesting may again be occurring. Fuller (1978), Williams *et al.* (1993), and Anthony and Downing (2001) speculated that declines in certain populations of mussels can be directly related to over-harvesting, with these mussels now present in low numbers due to their inability to recover from historical harvesting pressures.

While harvesting removes individuals of select species, a more recent threat to all unionid species is caused by the introduction of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771). With the recent introduction of *D. polymorpha* into Lake Pepin, there is a concern that it may cause declines in native mussel populations in the Upper Mississippi River as it has in other regions of North America (Ricciardi *et al.*, 1995; 1998; Hart, 1999; Hart *et al.*, 2001a, 2001b).

Because of concern that over-harvest of at least one unionid species, *Amblema plicata* (Say, 1817), may be occurring within Lake Pepin, a long-term monitoring study of mussel beds was initiated in 1990. Monitoring was undertaken to provide a quantitative assessment of unionid populations with each of seven mussel beds. An added dimension of this monitoring program became necessary with the introduction of *Dreissena polymorpha* into Lake Pepin. Therefore, this research was modified to include the measurement of population densities of *D. polymorpha* that are currently colonizing Lake Pepin.

METHODS

Study sites

Seven unionid mussel beds were sampled annually from 1990 to 1997 in Lake Pepin, Minnesota (Fig. 1). Sampled beds located within Lake Pepin were located near

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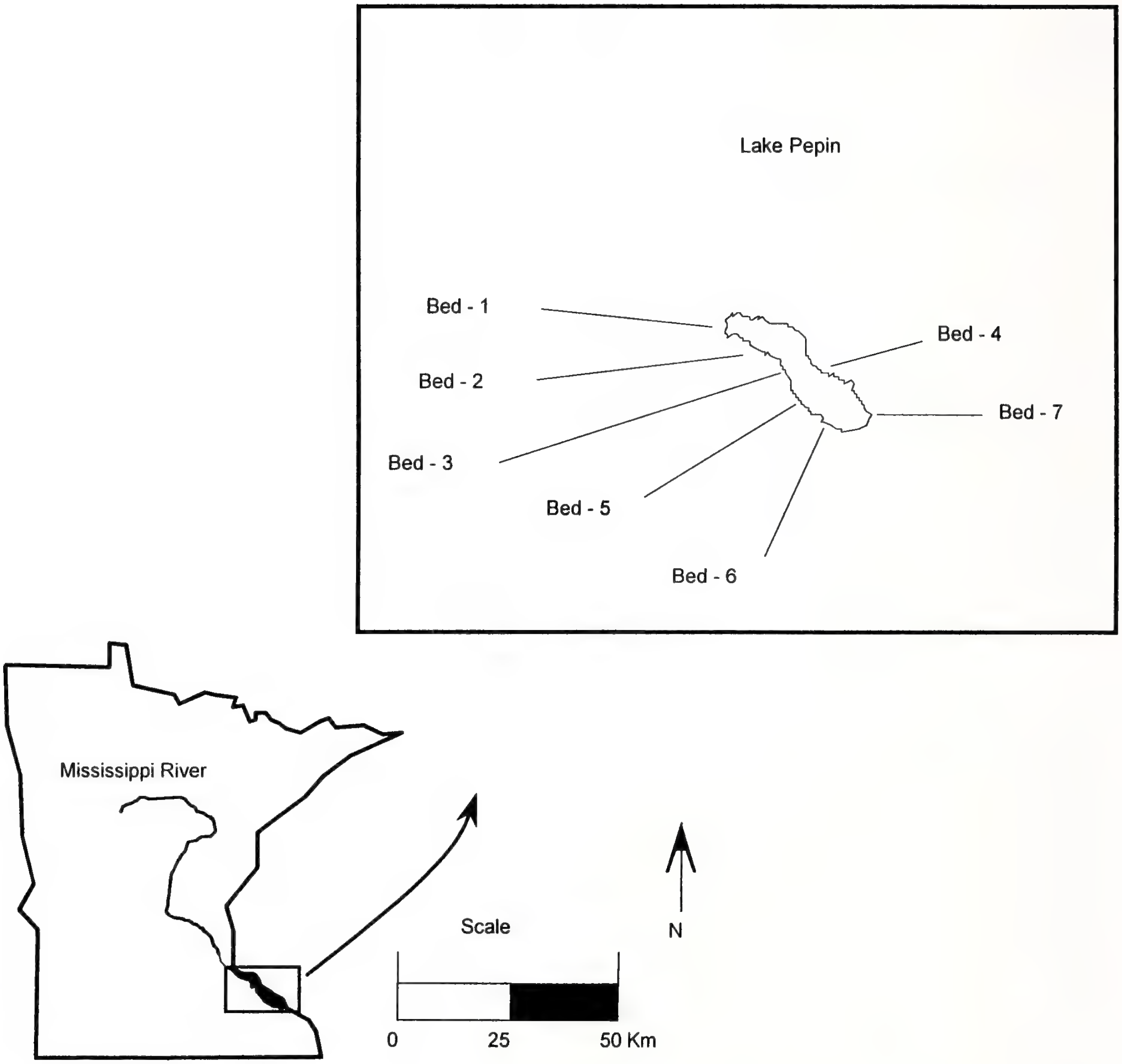

Fig. 1. Location of Lake Pepin between Minnesota and Wisconsin. Map inset shows locations of mussel beds where quantitative and qualitative samples were collected.

Fredrich's Point at Mississippi River Mile (MRM) 784.2 (Bed-1), Methodist Point at MRM 779.2 (Bed-2), Hok Si La at MRM 776 (Bed-3), Erickson's Point at MRM 775.5 (Bed-4), Waterman's at MRM 774 (Bed-5), King's Coulee at MRM 767.2 (Bed-6), and at the outlet of Lake Pepin along the Wisconsin shore across the river from Lacupolis, Minnesota, MRM 764.5 (Bed-7).

Mussel sampling

The quantitative methods that were used for the collection of unionid mussels during this study are outlined by Isom and Gooch (1986), Kovalak *et al.* (1986), Miller and Payne (1995), and references therein. Quantitative quadrat samples were collected at 7 beds by divers using SCUBA. At each bed, 3 subsites were randomly chosen for sampling. At each subsite, 10 randomly placed 0.25 m^2 aluminum quadrats were searched for mussels. Mussels were collected from within each of the quadrats either by placing all of the substrate, excavated to a depth of about 15 cm, into 20 L plastic pails and sieving the sample through a 0.6 cm^2 screen, or with the use of a suction dredge. When using the dredge, substrate from each quadrat was pumped to the surface, sieved through a 0.6 cm^2 screen, and searched for live mussels (Miller and Payne, 1995). All live mussels were removed from the screens and placed in labeled bags. Divers also collected qualitative samples during timed searches, placing all the mussels they encountered into mesh bags.

All collected mussels were identified, aged by counting the annual growth rings on the exterior of the shells' surfaces, measured for total shell length and height, and returned back into the substrate unharmed (Cvancara, 1970). Mussel identifications are based on taxonomic descriptions provided by Cummings and Mayer (1992). Taxonomy is that of Turgeon *et al.* (1998).

Data were analyzed using the statistical software program SYSTAT (Wilkinson *et al.*, 1992). A one-way analysis of variance and a post-hoc Tukey's multiple comparison technique were used to detect changes in mussel density over the course of this study.

While the weight of *Amblema plicata* harvested is of interest, a more useful management statistic is the number of individual *A. plicata* that are actually being removed from the Lake Pepin population. We developed regression equations for shell height vs. shell mass for *A. plicata* collected from both Minnesota and Wisconsin mussel beds. Using these regression equations we were able to calculate the number of legal-sized *A. plicata* per pound. This allowed us to estimate the number of individual *A. plicata* that have been harvested from Lake Pepin. Relationships between age, shell length, shell height, and shell mass of *A. plicata* were analyzed with the use of regression analysis (Zar, 1984). Linear, power, logarithmic, and exponential regression equations were investigated, and equations expressing the best fit to the data are presented (Smock, 1980).

RESULTS

The main goal of this research was to quantify changes within mussel beds. Therefore, we did not conduct statistical analyses on the differences among beds. The analysis of mussel community changes are presented with the upstream-most mussel beds and progressing sequentially to the downstream-most bed. While numerous mussel species may have been collected from a particular bed, we conducted statistical analysis only on those species that were present in sufficient enough numbers to warrant analysis (> 30 individuals collected).

Community composition

Twenty-nine unionid species were collected from the 7 mussel beds over the 8 years of this study. Bed-7, the downstream-most bed sampled, had the highest species richness, 29 species, compared to only 12 species at Bed-2, one of the most upstream beds sampled (Table 1, Fig. 1). Fourteen mussel species were collected from quantitative samples at Bed-1, while 12 mussel species were collected from Bed-2 during the study (Table 1). Both quantitative and qualitative sampling yielded 16 species in the Bed-3 community, while 15 mussel species comprised the Bed-4 community (Table 1). A total of 17 mussel species was collected from Bed-5 using both types of sampling, while the mussel community at Bed-6 comprised 13 species, and Bed-7 had 29 species (Table 1).

During the last year of quantitative sampling *Amblema plicata* remained the dominant mussel species in all beds sampled (Table 2). *Fusconaia flava* (Rafinesque, 1820) was the second most dominant mussel species in 5 of the 7 beds. *Elliptio dilatata* (Rafinesque, 1820), a species of special concern in the state of Minnesota, was the second most dominant mussel species in only one of the mussel beds (Bed-7) (Table 2). *Lampsilis siliquoidea* (Barnes, 1823), *Lampsilis cardium* (Rafinesque, 1820), and *Truncilla truncata* (Rafinesque, 1820), increased in dominance, while species such as *A. plicata*, and *Obliquaria reflexa* (Rafinesque, 1820), tended to decrease in dominance from upstream sites to downstream sites.

Mussel density

Densities of mussel communities ranged from a high of >70/m^2 at Bed-7 in 1993 to < 8/m^2 at Bed-5 in 1996 (Table 3). Densities of commercially harvested mussels, as well as protected species, did not show any appreciable changes in population density from 1995-97 within Bed-1 ($F = 2.677$, df=2, $p = 0.073$) (Table 3).

There was, however, a significant decline in mussel community density within Bed-2 over time ($F = 23.790$, df =3, $p<0.0001$) (Table 3). The mussel community density within Bed-3 was found to be declining over the course of this study ($F = 21.045$ df=4, $p<0.0001$) (Table 3). A decline in mussel community density was also measured in Bed-4 ($F = 3.315$, df=2, $p = 0.042$). Densities in Bed-4 in 1994 were 31.5/m^2, dropping to 21.3/m^2 in 1996 (Table 3). The community density of Bed-5 showed significant declines, decreasing from 19.6 mussels/m^2 in 1991, dropping to a low of 8.8/m^2 in 1996 ($F = 7.681$, df=3, $p<0.0001$) (Table 3). Mussel density within Bed-6 did not change significantly, remaining near 12 mussels/m^2 from 1995-97 ($F = 0.776$, df 2, $p = 0.463$) (Table 3). During this study Bed-7, the most downstream bed sampled, had the highest mussel densities measured within Lake Pepin. Density of this community was 70.6 mussels /m^2 in 1993, declining by 50%, to 34.7/m^2 in 1997 ($F=16.646$, df=3, $p<0.0001$) (Table 3).

Since reporting densities of all of the mussel species combined may be misleading, i.e., an increase in density of species A may mask a decrease in density of species B, we

Table 1. Live unionid species collected in quantitative and qualitative samples from Lake Pepin, Minnesota and Wisconsin, 1990 - 97.

	Mussel Beds[1]						
Mussel Species	1	2	3	4	5	6	7
Subfamily Ambleminae							
Megalonaias nervosa	x	x	x		x		x
Tritogonia verrucosa							x
Quadrula quadrula	x						
Quadrula metanevra					x		x
Quadrula pustulosa	x	x	x	x	x	x	x
Amblema plicata	x	x	x	x	x	x	x
Fusconaia flava	x	x	x	x	x	x	x
Cyclonaias tuberculata							x
Pleurobema coccineum					x		x
Elliptio diltata			x	x	x	x	x
Subfamily Anodontinae							
Utterbackia imbecillis	x	x	x	x	x		x
Pyganodon grandis		x	x			x	x
Stophitus undulatus			x		x		x
Alasmidonta marginata							x
Lasmigona complanata							x
Lasmigona costata							x
Subfamily Lampsilinae							
Obliquaria reflexa	x	x	x	x	x	x	x
Actinonaias ligamentina							x
Ellipsaria lineolata							x
Obovaria olivaria				x			x
Truncilla truncata	x	x	x	x	x	x	x
Truncilla donaciformis							x
Leptodea fragilis	x	x		x			x
Potamilus ohiensis	x	x	x	x	x	x	x
Potamilus alatus	x		x	x	x	x	x
Toxolasma parvus	x		x	x	x	x	x
Ligumia recta			x	x	x	x	x
Lampsilis siliquoidea	x	x	x	x	x	x	x
Lampsilis cardium	x	x	x	x	x	x	x
Total number of species collected	14	12	16	15	17	13	29

[1] Bed 1 = Fredrich's Point, bed 2 = Methodist Point, bed 3 = Hok Si La, bed 4 = Erickson's Point, bed 5 = Waterman's, bed 6 = King's Coulee, and bed 7 = Lacupolis.

separately analyzed species within the community to determine if species-specific density increases or declines were apparent. Likewise, because *Amblema plicata* is commercially harvested from Lake Pepin, we analyzed this species three ways; all *A. plicata* combined; individuals of legal harvest size (≥70 mm in shell height); and individuals of sub-legal size (< 70 mm in shell height).

Densities of all *Amblema plicata* remained stationary at only 2 of the beds, and declined at 5 of the 7 mussel beds sampled. Densities of *A. plicata* remained unchanged from 1995-97 within Bed-1 (F=0.809, df=2, P=0.448) (Table 3). Legal-sized *A. plicata* and individuals of sub-legal size remained unchanged as well (F = 0.617, df=2, p = 0.541, and F = 0.792, df=2, p = 0.456, respectively) (Table 1). Similarly, the density of *A. plicata* within Bed-6 did not change significantly during this study, remaining near 8/m^2 from 1995-1997 (F = 2.287, df=2, p = 0.108). Accordingly, both legal and sub-legal *A. plicata* densities did not change in any significant manner (F= 0.384, df=2, p=0.682, and F=1.807, df=2, p=0.170, respectively) (Table 3).

The overall change in mussel density in Bed-2 noted previously was most likely the result of declining population sizes of *Amblema plicata*. This population of *A. plicata* declined significantly from 1993-97 (F = 21.350, df=3, p<0.0001). Densities of this species within Bed-2 were 15.3/m^2 in 1993 compared to 5.1/m^2 in 1997 (Table 3). Legal-sized *A. plicata* did not decline (F = 0.851, df=3, p = 0.468), whereas sub-legal sized individuals did (F = 20.158, df=3, p<0.0001) (Table 3). Similar to Bed-2, densities of *A. plicata* within Bed-3 ranged from 21.8/m^2 in 1993 to 3.3/m^2 in 1997 (F = 14.940, df=4, p<0.0001). Densities of legal-sized individuals of *A. plicata* within Bed-3

Table 2. Percent occurrence of mussel species collected from quantitative samples during the last sampling event (1996 or 1997). Values are rounded to the nearest whole percentage point.

	Bed 1	Bed 2	Bed 3	Bed 4	Bed 5	Bed 6	Bed 7
Species	% occurrence	% occurrence	% occurrence	% occurrence	% occurrence	% occurrence	% occurrence
Amblema plicata	64	46	50	57	59	37	31
Fusconaia flava	6	32	24	12	19	34	5
Obliquaria reflexa	19	14	8	11	12	7	9
Utterbackia imbecillis	1	3	0	2	0	0	1
Truncilla truncata	8	2	10	12	4	12	14
Lampsilis siliquoidea	1	2	2	0	2	1	3
Toxolasma parvus	1	1	0	0	0	5	1
Quadrula pustulosa	1	1	2	2	1	1	1
Potamilus ohiensis	1	1	1	1	0	0	1
Pyganodon grandis	0	1	1	0	0	1	1
Strophitus undulatus	0	0	0	0	0	0	2
Quadrula quadrula	0	0	0	0	0	1	0
Potamilus alatus	0	0	0	0	0	0	1
Pleurobema coccineum	0	0	0	0	0	0	1
Megalonais nervosa	0	0	2	0	0	0	0
Leptodea fragilis	0	0	0	0	0	0	2
Lampsilis cardium	0	0	1	2	1	0	7
Ligumia recta	0	0	0	0	1	0	2
Elliptio dilatata	0	0	1	0	0	0	20

declined from 9.6/m^2 in 1990 to 0.8/m^2 in 1997 (F = 12.574, df=4, $p<0.0001$). Individuals < 70mm declined from 1993 to 1995-97 (F = 13.843, df=4, $p<0.0001$); however, multiple comparison tests revealed no differences in densities comparing 1990 to 1995-97 ($P>0.05$) (Table 3).

Mussel community density declines within Bed-4 were most likely due to changes in *Amblema plicata* densities. Densities of *A. plicata* declined from 18.3/m^2 and 19.3/m^2 in 1991 and 1994 to 12.3/m^2 in 1996 (F = 4.472, df=2, p = 0.015) (Table 3). While densities of legal-sized *A. plicata* did not change during this study (F = 1.432, df=2, p = 0.242) (Table 3), densities of sub-legal sized *A. plicata* declined from 17.6/m^2 in 1991 to 10.3/m^2 in 1996 (F = 6.567, df=2, p = 0.002).

The change in mussel community densities at Bed-5 can also be attributed to population declines of the harvested mussel species, *Amblema plicata*, which dropped from 11.8/m^2 in 1991 to 6.4/m^2 in 1997 (F = 6.228, df=3, p = 0.001). Legal-sized *A. plicata* did not show signs of population declines (F = 1.282, df=3, p = 0.285), yet individuals of sub-legal size in the population did (F = 5.575, df=3, p = 0.001) (Table 3).

Densities of all *Amblema plicata* in Bed-7 were 18.5/m^2 in 1993 and dropped to 7.7/m^2 in 1996 (F = 4.512, df=3, p = 0.005) (Table 3). Densities of both legal and sub-legal *A. plicata* in this bed also fluctuated during this study, albeit not significantly between some years (F = 2.873, df=3, p = 0.040, and F = 4.379, df=3, p = 0.006, respectively) (Table 3).

The population density of the commercial mussel species *Fusconaia flava* showed slight fluctuations or remained stationary at 5 of the 7 beds sampled, and declined at the other 2 beds sampled. Densities of *F. flava* in Bed-1 declined in 1997 compared to 1996, yet there was no significant difference in densities between 1995 and 1997 (F = 7.065, df=2, p = 0.001) (Table 3). Densities peaked with 3.07 mussels/m^2 in 1996 compared to a low of 0.7/m^2 in 1997. Similarly, *F. flava* in Bed-3 showed a significant decline in numbers during select years from 1990 to 1997 (F = 6.735, df=4, $p<0.0001$) (Table 3).

Fusconaia flava, a species legally harvested from Wisconsin waters of the Mississippi River, showed significant declines from 1993-97 within Bed-7 (F = 22.897, df=3, $p<0.0001$). Densities of this species declined from 9.7/m^2 in 1993 to 1.6/m^2 in 1996-97 (Table 3).

Fusconaia flava did not show any significant differences in density during this study in Bed-2 (F = 2.638, df=3, p = 0.052) (Table 3). Likewise, there were no significant differences in densities of *F. flava* detected from 1991 to 1996 in Bed-4. Densities within Bed-4 were 2.9/m^2 in 1991 and remained close to this level through 1996 (F = 0.292, df=2, p = 0.748) (Table 3). Unlike the commercially valuable *Amblema plicata*, it is illegal to harvest *F. flava* from Minnesota waters. Consequently *F. flava* did not show any significant declines in density from 1991-97 within Bed-5 (F = 0.870, df 3, p = 0.460) remaining near 2-3 individuals/m^2 (Table 3). Likewise, densities of *F. flava* did not show any significant changes during the time Bed-6 was studied, remaining near 2.5 - 4 mussels/m^2 from 1995-97 (F = 2.412, df=2, p = 0.096) (Table 3).

Although *Fusconaia flava* exhibited some density declines in Bed-1, *Obliquaria reflexa* did not. *Obliquaria*

Table 3. Mean density (± SE) comparisons of Lake Pepin unionid populations within mussel beds. Multiple comparisons are made using ANOVAs and Tukey's multiple comparison tests. Means are based on 30 replicate 0.25 m^2 quadrat samples.

	1990		1991		1993		1994		1995		1996		1997	
Site and Species	Mean (SE)[2]	Mult.[1] comp.	Mean (SE)[2]	Mult.[1] comp.	Mean (SE)[2]	Mult.[1] comp.	Mean (SE)[2]	Mult.[1] comp.	Mean (SE)[2]	Mult.[1] comp.	Mean (SE)[2]	Mult.[1] comp.	Mean (SE)[2]	Mult.[1] comp.
Bed-1														
All unionids									13.2 (1.69)	A	15.9 (1.17)	A	11.7 (1.02)	A
A. plicata									7.07 (0.83)	A	8.8 (1.11)	A	7.5 (0.76)	A
A. plicata > 70 mm^3									0.7 (0.34)	A	0.5 (0.25)	A	0.4 (0.16)	A
A. plicata < 70 mm^3									6.5 (0.83)	A	8.27 (1.03)	A	7.1 (0.76)	A
F. flava									2.3 (0.68)	AB	3.07 (0.71)	A	0.7 (0.25)	B
O. reflexa									2.7 (0.48)	A	2.13 (0.71)	A	2.2 (0.43)	A
Bed-2														
All unionids					27.1 (2.4)	A			25.7 (1.87)	AB	19.6 (1.69)	B	11.3 (0.98)	C
A. plicata					15.3 1.99)	A			15.7 (1.34)	A	9.5 (1.01)	B	5.1 (0.66)	C
A. plicata > 70 mm^3					0.53 (0.25)	A			0.8 (0.35)	A	0.27 (0.19)	A	0.4 (0.16)	A
A. plicata < 70 mm^3					14.8 (2.0)	A			14.8 (1.27)	A	9.6 (1.04)	B	4.8 (0.66)	C
F. flava					6.3 (0.93)	A			5.6 (0.44)	A	4.4 (0.78)	A	3.7 (0.59)	A
O. reflexa					4.3 (0.90)	A			3.47 (0.81)	AB	4.8 (0.82)	A	1.5 (0.34)	B
Bed-3														
All unionids	30.4 (5.69)	A			29.2 (4.3)	A			11.2 (1.53)	B	11.6 (1.24)	B	6.8 (0.65)	B
A. plicata	16.8 (3.76)	AB			21.8 (4.67)	A			6.0 (1.28)	BC	5.0 (0.76)	C	3.3 (0.56)	C
A. plicata > 70 mm^3	9.6 (3.59)	A			4.1 (1.17)	B			0.8 (0.35)	C	0.6 (0.34)	C	0.8 (0.23)	C
A. plicata < 70 mm^3	7.2 (0.99)	A			17.6 (3.53)	B			5.2 (1.09)	AC	4.4 (0.78)	AC	2.5 (0.49)	AC
F. flava	7.6 (1.83)	A			3.5 (0.83)	BC			4.1 (0.68)	AC	4.3 (0.85)	AC	1.7 (0.33)	B
O. reflexa	0.8 (0.53)	AB			0.27 (0.19)	A			0.27 (0.19)	A	1.4 (0.47)	B	0.53 (0.20)	AB
Bed-4														
All unionids			23.7 (2.05)	AB			31.5 (3.03)	A			21.3 (2.69)	B		
A. plicata			18.3 (1.7)	A			19.3 (1.76)	A			12.3 (1.79	B		

(continued)

Table 3. (continued)

Site and Species	1990 Mean (SE) [2]	1990 Mult. [1] comp.	1991 Mean (SE) [2]	1991 Mult. [1] comp.	1993 Mean (SE) [2]	1993 Mult. [1] comp.	1994 Mean (SE) [2]	1994 Mult. [1] comp.	1995 Mean (SE) [2]	1995 Mult. [1] comp.	1996 Mean (SE) [2]	1996 Mult. [1] comp.	1997 Mean (SE) [2]	1997 Mult. [1] comp.
A. plicata > 70 mm[3]			1.6 (0.45)	A			0.5 (0.34)	A			1.5 (0.41)	A		
A. plicata < 70 mm[3]			17.6 (1.72)	A			18.8 (1.92)	A			10.3 (1.8)	B		
F. flava			2.9 (0.81)	A			3.8 (1.00)	A			2.8 (0.72)	A		
O. reflexa			1.7 (0.42)	A			4.3 (0.85)	B			2.4 (0.65)	AB		
Bed-5														
All unionids			19.6 (3.00)	A			16.6 (1.77)	AB			8.8 (1.16)	C	10.8 (1.34)	BC
A. plicata			11.8 (2.40)	A			11.8 (1.65)	AB			4.8 (0.87)	C	6.4 (0.97)	BC
A. plicata > 70 mm[3]			1.8 (0.74)	A			2.3 (0.81)	A			0.9 (0.31)	A	1.2 (0.34)	A
A. plicata < 70 mm[3]			10 (2.08)	A			9.4 (1.66)	AC			3.9 (0.89)	B	5.1 (0.81)	BC
F. flava			2.8 (0.66	A			2.3 (1.09)	A			1.5 (0.41)	A	2.0 (0.53)	A
Bed-6														
All unionids									15.7 (1.36)	A	15.2 (1.81)	A	13.2 (1.33)	A
A. plicata									7.9 (1.08)	A	6.9 (1.08)	A	4.9 (0.78)	A
A. plicata > 70 mm[3]									0.93 (0.31)	A	0.8 (0.35)	A	0.5 (0.32)	A
A. plicata < 70 mm[3]									6.9 (1.08)	A	5.9 (0.95)	A	4.4 (0.78)	A
F. flava									2.5 (0.56)	A	4.7 (0.90)	A	4.5 (0.81)	A
O. reflexa									0.93 (0.31)	A	0.4 (0.22)	A	0.93 (0.37)	A
Bed-7														
All unionids					70.56 (4.79)	A			36.1 (4.36)	B	30.1 (2.86)	B	34.7 (4.10)	B
A. plicata					18.5 (2.74)	A			16.8 (2.74)	A	7.7 (1.47)	B	10.9 (2.23)	AB
A. plicata > 70 mm[3]					2.3 (0.77)	A			1.2 (0.48)	A	2.0 (0.76)	A	0.13 (0.13	A
A. plicata < 70 mm[3]					13.9 (2.64)	AB			15.6 (2.60)	AC	5.4 (1.09)	B	11.1 (2.23)	AB
F. flava					9.7 (1.48)	A			2.7 (0.62)	B	1.6 (0.41)	B	1.6 (0.53)	B
E. dilatata					9.9 (1.35)	A			7.1 (1.08)	A	8.9 (1.38)	A	6.8 (1.09)	A

[1] Means with a common letter within both sites and species are not significantly different, ($P>0.05$), using an ANOVA and Tukey's multiple comparison tests.

[2] (SE) equals standard error of the mean.

[3] Shell height in mm.

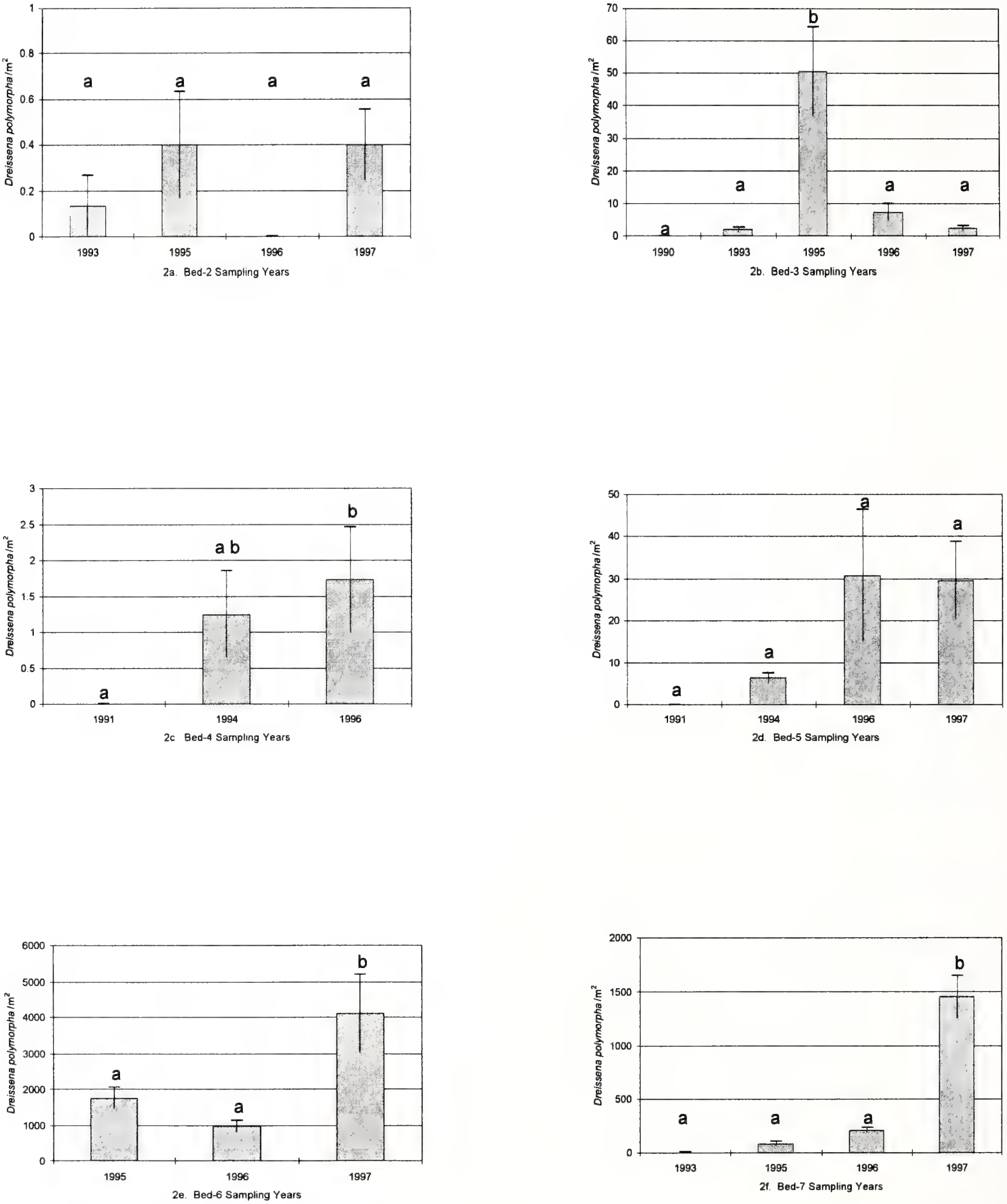

Fig. 2. Densities of *Dreissena polymorpha* measured in Beds 2-7. Similar letters above histograms indicate a lack of significant differences among years (mean ± 1 SE; ANOVA and Tukey's multiple comparison test, P>0.05).

reflexa densities were stable in Bed-1 from 1995-96, remaining near 2.5 mussels/m^2 (F = 0.247, df=2, p = 0.782) (Table 3). *Obliquaria reflexa* showed a somewhat different pattern in Bed-2 in that population densities gradually declined from 1993 to 1997 (F = 5.808, df=3, p = 0.001) (Table 3). The between-year fluctuations in density of *O. reflexa* in Bed-3 were similar to those of *F. flava* in that there were some significant differences between years; densities in 1990 and 1997 were 0.8/m^2 and 0.53/m^2, respectively (F = 2.570, df=4, p = 0.04) (Table 3). *Obliquaria reflexa* in Bed-4 showed slight changes in density during this study (F = 3.507, df=2, p = 0.035). Densities in Bed-4 were 1.7/m^2 in 1991, increasing to 4.3/m^2 in 1994, and declining again to 2.4/m^2 in 1996 (Table 3).

Densities of *Obliquaria reflexa* in Bed-6 were much the same throughout this study. Its densities have been rather stable, albeit low, < 1 mussel/m^2, with no significant differences being detected from 1995-97 (F = 1.002, df=2, p = 0.371) (Table 3).

Elliptio dilatata, a species found in large numbers only in Bed-7, did not change significantly in population density from 1993-1997 (F = 1.327, df=2, p = 0.270). Densities of this species within Bed-7 stayed near 7-9 mussels/m^2 throughout the present study (Table 3).

Dreissena polymorpha was initially collected from Bed-1 in 1995 and has been found in low numbers since that time, <0.03/m^2. *Dreissena polymorpha* was initially collected from Bed-2 in 1993, and was present in low numbers through 1997, although densities did not change significantly (F = 1.431, df=3, p = 0.236) (Fig. 2a). However, there were significant differences in densities of *D. polymorpha* at Bed-3, declining from a peak of 50/m^2 in 1995 to <10/m^2 in 1997 (F = 12.119, df=4, p<0.0001) (Fig. 2b). *Dreissena polymorpha* was first collected in 1994 in Bed-4, yet densities did not significantly increase during this study (F = 3.076, df=2, p = 0.052) (Fig. 2c). Likewise, *D. polymorpha* was first found in low numbers in Bed-5 in 1991, and population densities did not change significantly from 1991-97 (F = 1.769, df=3, p = 0.159) (Fig. 2d).

The greatest change in the mussel community noted within Bed-6 was the increase in density of *Dreissena polymorpha*. Densities within Bed-6 were >1,700 mussels/m^2 in 1995, increasing to over 4,100 mussels/m^2 in 1997 (F = 6.314, df=2, p = 0.003) (Fig. 2e). *Dreissena polymorpha* is still increasing in this bed, as we have noted large numbers of newly settled individuals during the summers of 1999 and 2000 (Hart and Davis, personal observation). In the species rich Bed-7 community, *D. polymorpha* was first collected in 1993, and densities have been increasing since their initial occurrence (F = 39.173, df=3, p<0.0001). *Dreissena polymorpha* increased from less than 4/m^2 in 1993 to over 1,400/m^2 in 1997 (Fig. 2f).

Amblema plicata recruitment

Because one of the objectives of this study was to assess the health of the *Amblema plicata* populations in Lake Pepin, we noted the occurrence of young *A. plicata* within the study areas. Shell height distributions of *A. plicata* indicated recent recruitment into the studied populations is occurring only at low levels.

We measured small numbers of young individuals within several of the sampled beds, but most populations were dominated by older individuals, indicating that significant recent recruitment has not occurred. Histograms of shell height from Bed-3 and Bed-7 (Figures 3 and 4 respectively) illustrate typical shell height distributions of *Amblema plicata* measured within all of the mussel beds sampled during this study.

Using Minnesota data (Hart, 1999), the number of legal-sized *Amblema plicata* per pound equaled 2.03 individuals (Fig. 5), while the number of individuals per pound using Wisconsin regression equations (Hart, 1999; Fig. 6) equaled 2.08. Using the harvest records acquired from the Minnesota and Wisconsin Departments of Natural Resources (Fig. 7) (Welke and Miller, 1990; Hart, 1999; Minnesota and Wisconsin DNR unpublished data) and the regression equations we developed, we estimate that about 254,000 live mussels were harvested from the Minnesota side of Lake Pepin in 1993, and an additional 750,000 mussels were taken from the Wisconsin side in 1990.

DISCUSSION

Lake Pepin still harbors a diverse mussel assemblage. Twenty-nine living unionid species were collected from this portion of the Mississippi River. The downstream-most mussel bed sampled, Bed-7, possessed a community with populations of all of the species that were collected from Lake Pepin during the present study. We also observed that the numbers of mussel species living within Lake Pepin tended to increase from upstream to downstream. The upstream and mid-lake habitats of Lake Pepin have been impacted more by water quality and habitat degradation (Ellis, 1931; Thiel, 1981), when compared to those downstream. This is particularly true of Bed-7, which is at the outlet of Lake Pepin and is more a "riverine" habitat, benefitting from the sediment settling effects of the lake. This difference in habitats may explain in part why the downstream portion of the lake supports a more diverse mussel community at this time. The downstream-most mussel bed sampled not only had the most species present, but also had the highest density of all beds sampled. However, this bed, as well as four additional beds sampled, showed population density declines for some of the mussel species that inhabit these areas.

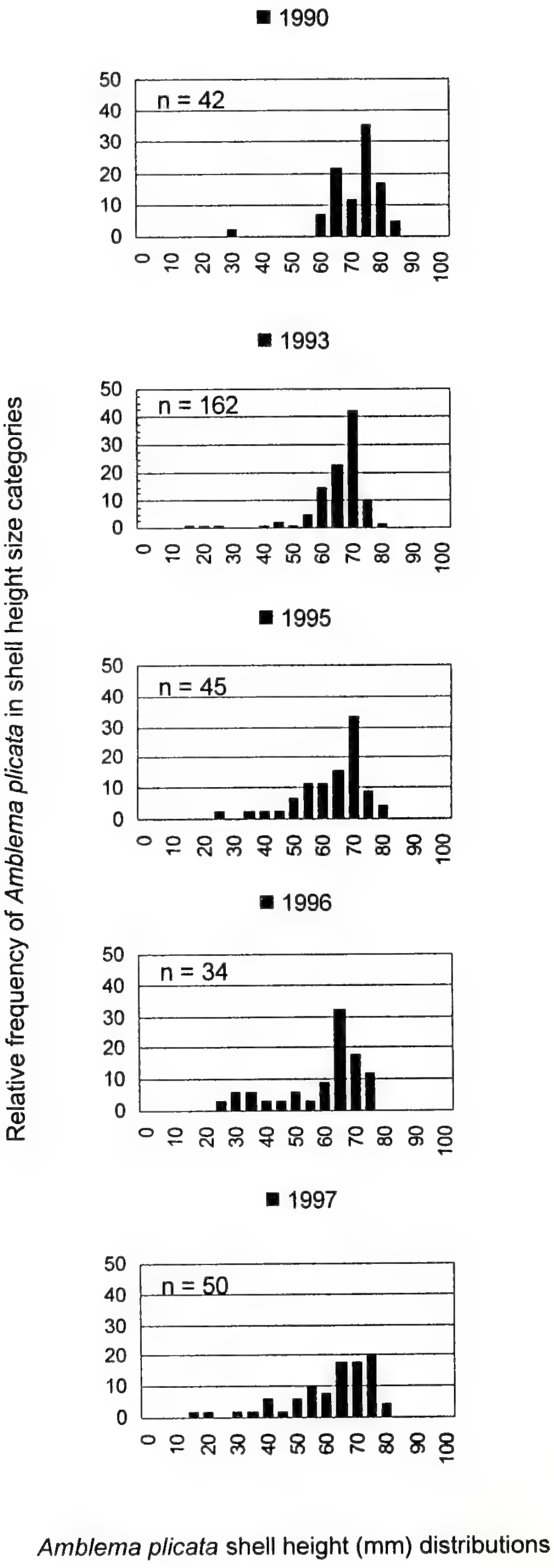

Fig. 3. Shell height distributions of *Amblema plicata* measured in Bed-3 in 1990, 1993, and 1995-1997. The values on the x axis are the midpoints for the distribution ranges.

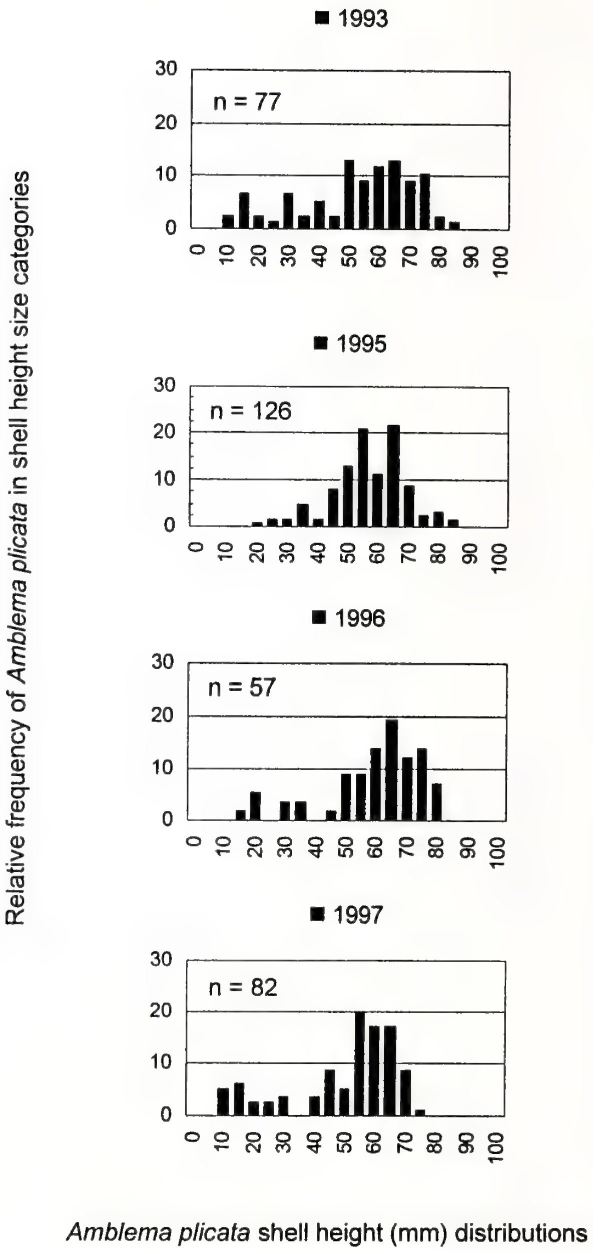

Fig. 4. Shell height distributions of *Amblema plicata* measured in Bed-7 in 1993 and 1995-1997. The values on the x axis are the midpoints for the distribution ranges.

Southall (1925) reported that during the early part of the 1900's, 35% of the Lake Pepin mussel community was comprised of the Lake Pepin mucket (*Lampsilis pepinensis*, now *Lampsilis siliquoidea* [Barnes, 1823]). Today *L. siliquoidea* is only represented as a minor component of the Lake Pepin mussel assemblage, making up less than 3% of the communities we sampled. The change in community dominance and density of *L. siliquoidea* within the Lake Pepin mussel assemblage was attributed to their commercial harvest for pearl buttons (Southall, 1925). Past harvesting pressure seems to be the most likely cause for the low numbers of this species as the present habitat conditions in Lake Pepin are favorable for *L. siliquoidea* (Hart, 1995). Currently the dominant mussel in the Lake Pepin community is the commercially harvested *Amblema plicata.* Yet its community dominance appears to be changing much as *L. siliquoidea* did.

Amblema plicata showed significant declines at 5 of the 7 mussel beds sampled during this study. At several of these sites density declines as great as 50% were detected. The most notable decline occurred at Bed-3 where densities of legal-sized *A. plicata* declined from a high of 9/m^2 to about 0.8 mussels/m^2 over the course of the present study. The most plausible explanation for the declines in legal sized individuals that we measured is their removal by commercial harvesters. We believe that the decline can be attributed to harvest because the mean annual survival of *A. plicata*, as well as other unionids in the habitats studied in Lake Pepin, has been shown to be relatively high in natural habitats (≥90%) (Hart, 1999; Hart *et al.*, 2001b), and large numbers of fresh dead *A. plicata* were not collected from any of these 5 mussel beds during routine sampling (Hart and Davis, personal observation). The lack of fresh dead individuals found at these sites indicate that the decline in population densities is not due to *Dreissena polymorpha.* We further believe that the declines in sub-legal sized *A. plicata* indicate that these individuals are either being harvested illegally or are being removed from the population when they grow into the legal harvest-size slot and are not being replaced by recruitment of new individuals into the population. The decline in densities we measured is the result of these individuals being physically removed from the populations. This type of population response, i.e., declining average sizes near to or at the age of first reproduction (Anthony and Downing, 2001), which is about 8 years of age for *A. plicata,* is typical for exploited populations. Large numbers of commercial harvesters were seen working at Beds 3 and 7 during the late 1980s (Davis, personal observation), and harvesters were often present during the summer months of this research project (Hart, personal observation).

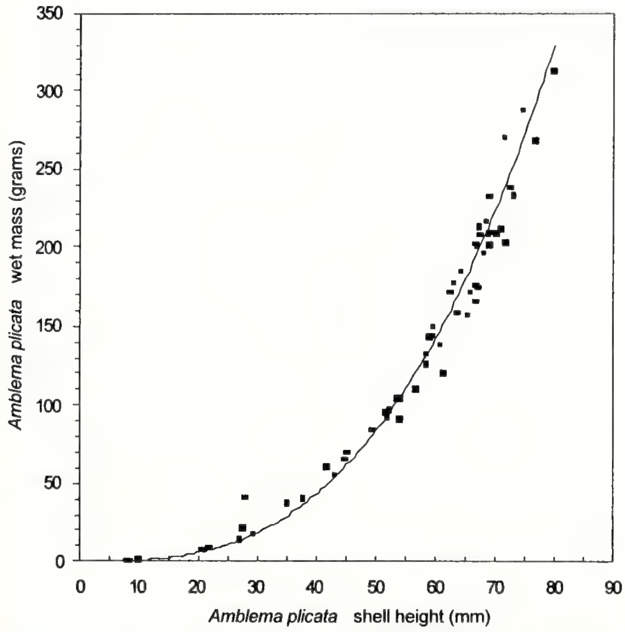

Fig. 5. Shell height vs. mass relationships of *Amblema plicata* measured in Bed-5 (Minnesota) (Hart, 1999). Power equation regression line fit to the data points equals: *Amblema plicata* shell mass = 0.0009(shell height)$^{2.9336}$. R^2 = 0.9864.

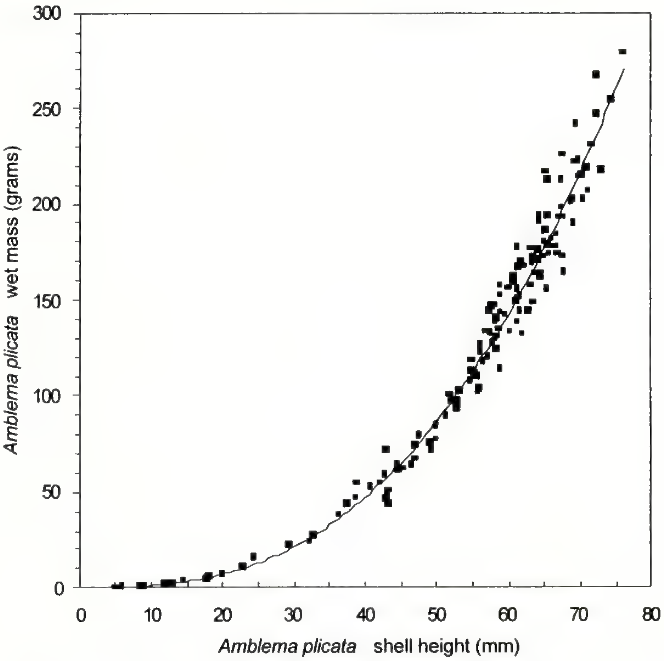

Fig. 6. Shell height vs. mass relationships of *Amblema plicata* measured in Bed-4 (Wisconsin) (Hart, 1999). Power equation regression line fit to the data points equals: *Amblema plicata* shell mass = 0.0021(shell height)$^{2.7218}$. R^2 = 0.9892.

The other noteworthy change in the population structure of *Amblema plicata* came from Bed-7, where densities of this species were over 18 mussels/m^2 in the early 1990s and declined to less than 9/m^2 during the late 1990s. During this study this mussel bed was harvested for not only *A. plicata*, but also *Fusconaia flava* (Hart, personal observation). Densities of *F. flava* also declined at this bed, where densities were over 9/m^2 during 1991, declining to 2/m^2 in 1997.

While *Fusconaia flava* are legal to harvest from Wisconsin border waters, it is not legal to harvest this species in Minnesota. Densities of *F. flava* did not vary much at 4 of the 5 Minnesota beds studied. Other non-harvested mussel species, in both Minnesota and Wisconsin, showed either stationary or fluctuating densities during the time this study was conducted.

An assessment of the mussel harvest in the Mississippi River (Welke and Miller, 1990) revealed that over 360,000 pounds of live *Amblema plicata* were harvested from the Wisconsin portion of Lake Pepin in 1990. Welke and Miller (1990) speculated that this intense harvesting pressure could depress mussel stocks for several years. Minnesota Department of Natural Resources records since 1990 document the harvest of *A. plicata* from the Minnesota beds of Lake Pepin. These records reveal intense harvesting occurred in Minnesota waters as well. Harvest from Minnesota peaked in 1993, with approximately 125,000 pounds of mussels harvested (Minnesota Department of Natural Resources, unpublished data; Hart, 1999) (Fig. 7).

While the poundage of *A. plicata* harvested is of interest, a more useful management statistic is the number of individual *A. plicata* that are actually being removed from the Lake Pepin population. Applying the results of the regression equations we developed, we estimated that each pound of collected mussels equaled about two individuals. Therefore, using the harvest records from Lake Pepin and the results of the regression equations, we estimate that about 254,000 live mussels were harvested from the Minnesota side of Lake Pepin in 1993, and an additional 750,000 mussels were taken from the Wisconsin side in 1990. Given the large numbers of individuals removed from the lake in just these two years, as well as the findings of this study documenting declining population densities of *A. plicata* in Lake Pepin, Welke and Miller's (1990) concern that populations of this species may be reduced seems to be borne out. The constant population densities of non-harvested species and the decreasing populations of harvested species implicate commercial harvesting as a factor in these declines.

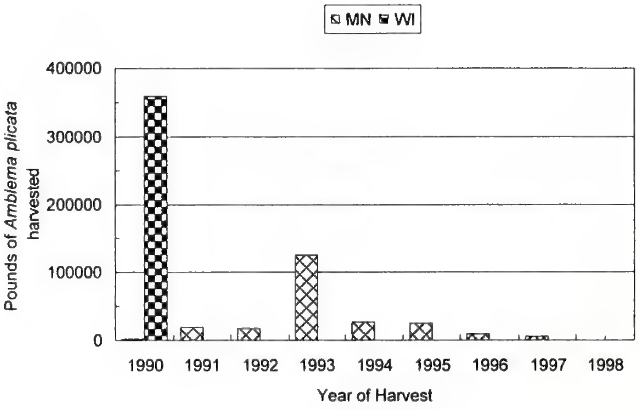

Fig. 7. Pounds of *Amblema plicata* harvested from Lake Pepin, Minnesota (Minnesota DNR unpublished data; Hart, 1999) and Wisconsin (Welke and Miller, 1990).

The ramifications of the harvesting of other molluscs have also been well documented. Declines in the commercially valuable mollusc, the black abalone (*Haliotis cracherodii*, Leach, 1814), in coastal California regions were attributed to their over-harvest (Richards and Davis, 1993). Much as we believe is occurring with *A. plicata* in Lake Pepin, *H. cracherodii* began to decline when increases in harvest occurred and recruitment could not keep pace with their removal (Richards and Davis, 1993). Heath *et al.* (1988) reported that there has been a steady decline in the commercially harvested washboard mussel, *Megalonaias nervosa* (Rafinesque, 1820), from some pools of the Upper Mississippi River. Commercial harvesting was implicated as a factor in the decline of *M. nervosa* because high levels of harvest had been documented, while low or no recruitment into the populations was evident (Heath *et al.*, 1988).

Size distributions of the *Amblema plicata* populations sampled during the present study indicate that there are very low levels of recruitment occurring for this species as well. Since *A. plicata* are like other long-lived organisms, sporadic recruitment may be able to maintain a population (Congdon *et al.*, 1994). However, sporadic recruitment was not readily detectable in appreciable numbers within most of the mussel beds we studied even though total substrate removal techniques were used to facilitate the collection of small individuals.

An additional factor that must be considered is not only the fate of *Amblema plicata* populations, but of all of the mussel species residing in Lake Pepin, in the presence of increasing densities of *Dreissena polymorpha*. This exotic invader was first found in Lake Pepin in 1990 and has since become widespread and dominant in the lower one-half to one-third of the lake (Hart, 1999; James *et al.*, 2000).

Densities of *Dreissena polymorpha* did decline at one of the mussel beds for unknown reasons. Possible causes for this decline may include a loss of a veliger source to repopulate the bed or changes in the chemical composition of the water above the bed (Mellina and Rasmussen, 1994). The first explanation seems most plausible, since densities of *D. polymorpha* were found to be lower in the upstream portion of the lake. Consequently, a large veliger source has yet to be located above this particular mussel bed (Hart and Davis, personal observation). As of 2000, *D. polymorpha* is found in excess of 20,000 individuals/m^2 in the lower one-third of the lake (Davis, personal observation). Densities of *D. polymorpha* at sampled mussel beds in this region of the lake are increasing rapidly, completely covering some portions of the lake bottom (Hart, 1999;

James *et al.*, 2000). Measurements of survival rates of native mussels in Lake Pepin indicate that, as in other parts of *D. polymorpha's* North American range (Haag *et al.*, 1993; Gillis and Mackie, 1994), *D. polymorpha* colonization is beginning to play a role in the decline of native mussel populations (Hart, 1999; Hart *et al.*, 2001a, 2001b).

Unfortunately, while declines in some population densities of unionid mussels, especially *Amblema plicata*, in Lake Pepin can be directly attributed to infestations of *Dreissena polymorpha* at this time (Hart, 1999), this mortality factor, unlike commercial harvest, cannot be controlled by natural resource managers. Furthermore, if the population declines that we measured were a direct result of *D. polymorpha*, we would have measured declines in all size classes of *Amblema plicata* as well as declines in population densities of non-harvested species. During this research this broad decline in mussel populations was not evident. Declines in the populations we studied were selective, i.e., most of the declines were attributed to loss of harvest-sized or near harvest-sized *A. plicata*, and not the other species in the community. Therefore, additional research is needed to determine the harvest impact upon *A. plicata* in the Upper Mississippi River, in particular Lake Pepin. This additional research should include a comprehensive population estimate of *A. plicata* in Lake Pepin that could be used in conjunction with recent estimates of *D. polymorpha* densities in Lake Pepin (James *et al.*, 2000). The findings of the present study, along with population estimates of *A. plicata* and *D. polymorpha*, should be incorporated into management objectives and harvest regulations formulated to ensure the continued survival of the unionid mussel communities residing in Lake Pepin.

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A new species of *Conocardium* Bronn, 1834 (Mollusca: Rostroconchia) from the Mississippian of Missouri, U. S. A.

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Abstract: The rostroconch *Conocardium formosum* n. sp. is described from the Mississippian (Chesterian) of Missouri. The narrow, elongate shape of the shell is different from all other known North American species of the genus.

Key Words: Mollusca, Rostroconchia, Mississippian, Missouri

Numerous reports on North American Mississippian rostroconchs have appeared, among which are: Hall (1856, 1883); Winchell (1862, 1870); White and Whitfield (1862); Whitfield (1882); Herrick (1888a, b); Miller (1892); Rowley (1900); Beede (1906); Girty (1910); Weller (1916, 1921); Branson (1942, 1958); Pojeta and Runnegar (1976); and Hoare (1990). Species of *Conocardium* s.s. were included in many of these reports but only that of Pojeta and Runnegar (1976) included narrowly elongate forms of the genus. These authors illustrated but did not describe two specimens, one Pennsylvanian and one Mississippian in age, designating both as *Conocardium* aff. *C. elongatum* (Sowerby, 1815). *Conocardium elongatum* is a Lower Carboniferous (Mississippian) species known from England and is quite different from the American Mississippian species described herein.

The holotype is in the collections of the National Museum of Natural History (USNM).

SYSTEMATICS

Class Rostroconchia Pojeta, Runnegar, Morris, and Newell, 1972
Order Conocardioida Neumayr, 1891
Superfamily Conocardiacea Miller, 1889
Family Conocardiidae Miller, 1889
Genus *Conocardium* Bronn, 1834
Conocardium formosum, new species
Fig. 1

Conocardium aff. *C. elongatum* (Sowerby). Pojeta and Runnegar, 1976, p. 70, pl. 38, figs. 4-7.

Diagnosis. Narrowly elongate shell with distinct separation of body and snout; strongly developed folded wing-like structure dorsally and laterally on snout.

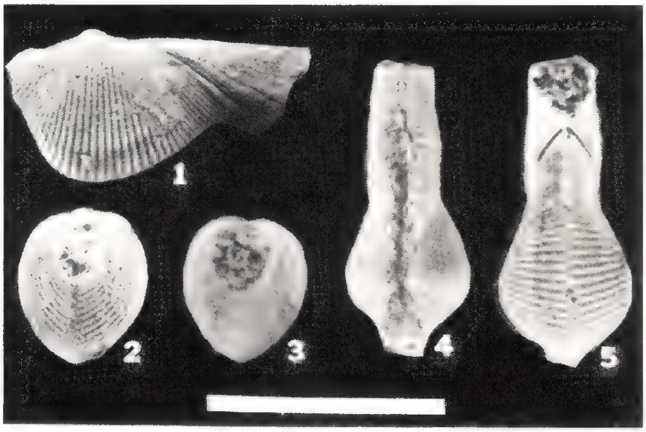

Fig. 1. *Conocardium formosum* n. sp. 1-5, holotype, right lateral, posterior, anterior, dorsal, and ventral views. Carterville Formation, Missouri. USNM 209298 (scale bar = 1 cm).

Description. Elongate, narrow, body distinct from snout; sides of snout subparallel; umbonal areas extend slightly above hinge line; dorsal margin slopes ventrally from beak area both posteriorly and anteriorly; ventral margin of body convex below beaks becoming straighter towards rostum and snout, curves sharply ventrally meeting snout area anteriorly; anterior gape subcircular, restricted to anterior extremity; posterior orifice lacking; rostrum suboval in cross section, length unknown; rostral face and body with 29 even-sized, rounded, closely-spaced, radial costae with narrow interspaces followed anteriorly by 10 fine more widely spaced costae; snout ornamentation begins at beak area as a V-shaped, folded, wing-like structure expanding anteriorly on dorsal and lateral surfaces, marked ventrally by four coarse costae followed dorsally by five or more fine, widely-spaced costae; ventrally, snout ornamentation forms an inverted V-shaped margin with radial costae near anterior gape; inner shelves not visible.

Measurements. Length, not including rostrum, 13.1 mm; width, 5.1 mm; height, 6.8 mm.

Etymology. Latin, *formosum*, beautifully formed.

Type. Holotype, USNM 209298.

Occurrence. Upper Carterville Formation (Mississippian, Chesterian) in mine dump near Duenweg, Missouri.

Discussion. *Conocardium formosum* differs from *C. elongatum* (Sowerby, 1815) by the presence of a more sharply set-off wing-like structure on the snout, a more abruptly curved rostral face, a narrower, more distinctly separated snout from the body, and sides of snout subparallel not converging anteriorly. Other Chesterian species that have been described (e. g. *C. peculiare* Girty, 1910; *C. chesterensis* Weller, 1921) are not as elongate and have much smaller length/height ratios as is the case for all other Mississippian species of the genus known in North America.

The folded wing-like structure on the snout of *Conocardium formosum* is similar to the structure present on the snout of species of the genus *Arceodomus* Pojeta and Runnegar, 1976. *Arceodomus* has a thin, relatively smooth outer shell layer covering the radial costae on the body. No trace of such an outer layer is present on the holotype of *C. formosum*. The ornamentation on the snout of the Pennsylvanian *Arceodomus prolata* Hoare and Mapes, 1990, differs significantly from that of *C. formosum* in having coarser, evenly-sized and spaced radial costae with intervening fine radial and transverse lirae.

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The Cruises of the *Eolis*: John B. Henderson's mollusc collections off the Florida Keys, 1910-1916*

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Abstract: John B. Henderson Jr.'s dredging expeditions off the Florida Keys, between 1910 and 1916, resulted in the most important and most extensive collection to date of benthic marine molluscs from the southeastern United States. The annual cruises aboard his private motor yacht *Eolis*, accompanied by malacologists Paul Bartsch, George Hubbard Clapp, and Charles Torrey Simpson, sampled extensively in various water depths from Miami to the Dry Tortugas, the westernmost extension of the Florida Keys island chain. Henderson deposited tens of thousands of specimen series in the collection of the Smithsonian Institution's National Museum of Natural History (NMNH) that are the basis of numerous malacological studies and were included in systematic papers by Dall, Bartsch, Henderson, Simpson, Pérez Farfante, Abbott, Boss, and many others. No cruise descriptions or station lists have been published to date; previous authors relied on unpublished *Eolis* "station lists" on file in the NMNH Department of Invertebrate Zoology. This paper provides for the first time a review of Henderson's original handwritten ship logs, now maintained in the Smithsonian Institution Archives. Based on these and other available sources, it reconstructs and corrects prior data about the *Eolis* cruises while providing insight into collecting conditions during the early 20th century. Most notably, it is shown that the Smithsonian *Eolis* station numbers reflect a sequence of specimen donations and accessions, rather than mirroring the actual cruise events either by sample number or date.

Key Words: Mollusca, expeditions, collections

> "We have much to learn yet of the habitats and stations of the mollusks" (J. B. Henderson, Jr., *Eolis* log entry, Key West, 30 May 1911)

The marine molluscan fauna of the southernmost tip of the continental United States is highly diverse, comprising in the vicinity of the Florida Keys island chain (recently protected as the 10,000 km^2 Florida Keys National Marine Sanctuary) more than 1,400 species (Mikkelsen and Bieler, 2000). Through the activities of numerous shell collectors and particularly through the popular shell books by R. Tucker Abbott (e. g., 1974; who frequently featured specimens from the Florida Keys in his illustrations), the near-shore molluscs from this region have become widely known. Systematic exploration - as opposed to casual beach collecting - of this region, however, has a surprisingly short history. The first attempt was by William Stimpson (1832-1872), who served initially as invertebrate zoologist at the United States National Museum (USNM; now the National Museum of Natural History [NMNH]), and after 1866, as director of the Chicago Academy of Sciences. In Chicago, he accumulated loans from U. S. and European museums in preparation for a major monograph of marine east-coast invertebrates. These loans included large parts of the Smithsonian collection of eastern American shells and alcohol-preserved molluscs which he had brought with him to Chicago. Among these were the original collections from the Straits of Florida and the Pourtalés Plateau off the Florida Keys obtained by Count Louis Francois de Pourtalés (of the Museum of Comparative Zoology, Harvard University) during the U. S. Coast Survey expeditions of the 1860s (Dall, 1896; Rehder, 1999). All of this material, together with the near-completed manuscript, were lost in the Great Fire of 1871 that devastated Chicago (Dall, 1883).[1] Referring to this loss, Dall (1883: 318) stressed that the "marine fauna of the American coast south from Cape Hatteras and thence to the Mexico-Texan border is at present less known than that of any other part of the coast of North America."

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*Supplementary materials, including station lists, available at the AMB web site <http://erato.acnatsci.org/ams/amspubs.html>), as well as the authors' home institution sites]

[1] Some of this lost material was subsequently cited by Dall, who had studied it briefly before it was sent to Stimpson. In fact, Dall described *Haliotis pourtalesii* n. sp. from memory — ten years after the only known specimen had been lost in the Chicago fire (Dall, 1881). It would take another 30 years before Henderson's *Eolis* cruise would find a second specimen (Henderson, 1911b).

"Under these circumstances, believing it better to make some sort of start at cataloging the shells of our southern coasts," William Healey Dall (1883: 320) began anew by describing the results of collecting efforts in the Florida Keys by amateur conchologist Henry Hemphill (1830-1914) and discussed the sparse earlier literature for the region, including the papers of James C. Melvill (1881; who reported on material obtained mainly in Key West during 1871 and 1872) and W. W. Calkins (1878; who collected in the region during 1875 and 1877). Subsequently, Dall described and summarized the renewed dredging efforts of the U. S. Coast Survey, this time by the Steamer *Blake*, off southern Florida (Dall, 1886, 1889a), culminating in a preliminary species catalog (Dall, 1889b).

This comprised the modest background knowledge when a private shell collector, John Brooks Henderson, Jr., set out to collect in the waters off the Florida Keys. His efforts, between 1910 and 1916, resulted in the most important 20th-century collection of marine molluscs in the southeastern United States. There is hardly (and will hardly ever be) a serious study of western Atlantic molluscs that does not make reference to Henderson's *Eolis* material. However, surprisingly, except for brief descriptions of invidual collecting events by Henderson (1911a, b, 1913, 1914) and a short summary by Abbott (1950), no published account exists of these expeditions.

John Brooks Henderson, Jr. (1870-1923) (Fig. 1), the son of lawyer and United States Senator (Missouri) John Brooks and author Mary Foote Henderson, graduated from Harvard University in 1891 and Columbian Law School (now George Washington University) in 1893. He served briefly (1896-1897) as secretary to John W. Foster, a diplomatic advisor to the Chinese government. In 1897 he traveled with General Nelson A. Miles on a tour of Europe and the Ottoman Empire as a civilian observer of the armies of the great European powers (Anonymous, 1923; Abbott, 1976: 191). Like his father before him, he was appointed a citizen member of the Smithsonian Institution Board of Regents in 1911 and retained that post until his death (SIRIS, February 2002). Interested in shells since his youth, he collected molluscs in Jamaica, Haiti, Cuba, the Lesser Antilles, Hawaii, the United States, Europe, Japan, and China, and published 43 articles on molluscs, most of which appeared in *The Nautilus* and the *Proceedings of the United States National Museum*. He also compiled the first index volume for *The Nautilus* (Henderson, 1927).[2] His most significant published malacological work is "A Monograph of the East American Scaphopod Mollusks" (Henderson, 1920a). Throughout his 30-year association with the USNM, he personally financed collecting expeditions and the purchase of several collections, was assigned his own desk space, supported an assistant, and ultimately donated the majority of his self-collected specimens to the Smithsonian's Division of Mollusks (Rehder, 1999).

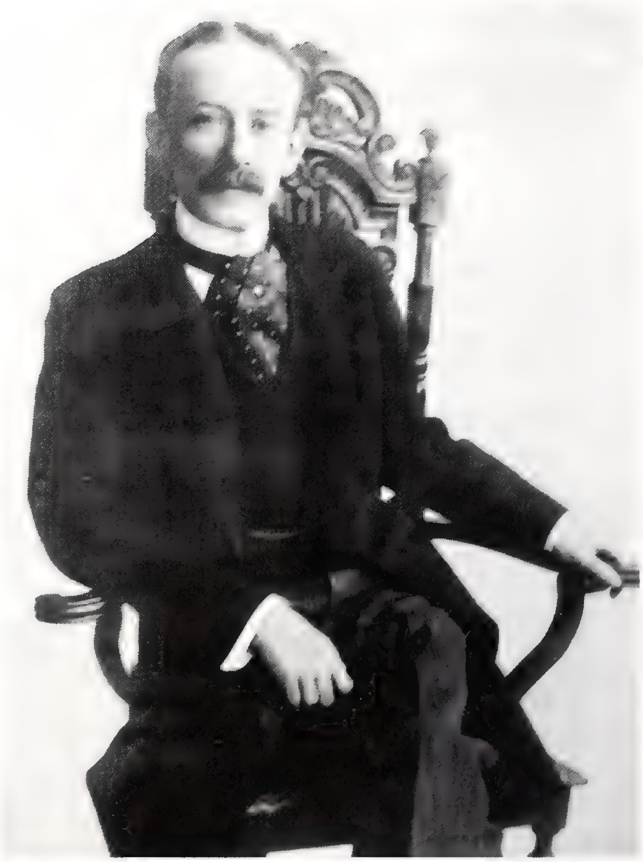

Fig. 1. John B. Henderson, Jr. Reproduction of portrait in the Division of Mollusks, NMNH (Smithsonian Institution Archives SIA 7418).

In 1909, the 15-ton motor yacht *Eolis* was built for Henderson, with Washington, D. C., as her homeport. The vessel was 50 feet (15 m) in length, 11 feet in width, and drew 5 feet of water. She was specifically designed for the purpose of dredging molluscs in western Atlantic waters, complete with a launch (the *Leda*), a smaller tender, a winch, a table sieve, and sleeping accommodations for at least five men.

Henderson made five annual spring cruises to the Florida Keys (Fig. 2) between 1910 and 1916 (his 1912 cruise was to Miami and Bimini, Bahamas, and 1914 was spent aboard the *Tomas Barrera* off Cuba, resulting in a published narrative (Henderson, 1916; see also Turner, 1950)]. According to Abbott (1950: 219), the five Florida cruises between 1910 and 1915 (including 1912 off Miami) resulted in "31,400 lots of deep-sea mollusks" that were

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[2] Dedicated to J. B. Henderson, with 1916 photograph as frontispiece.

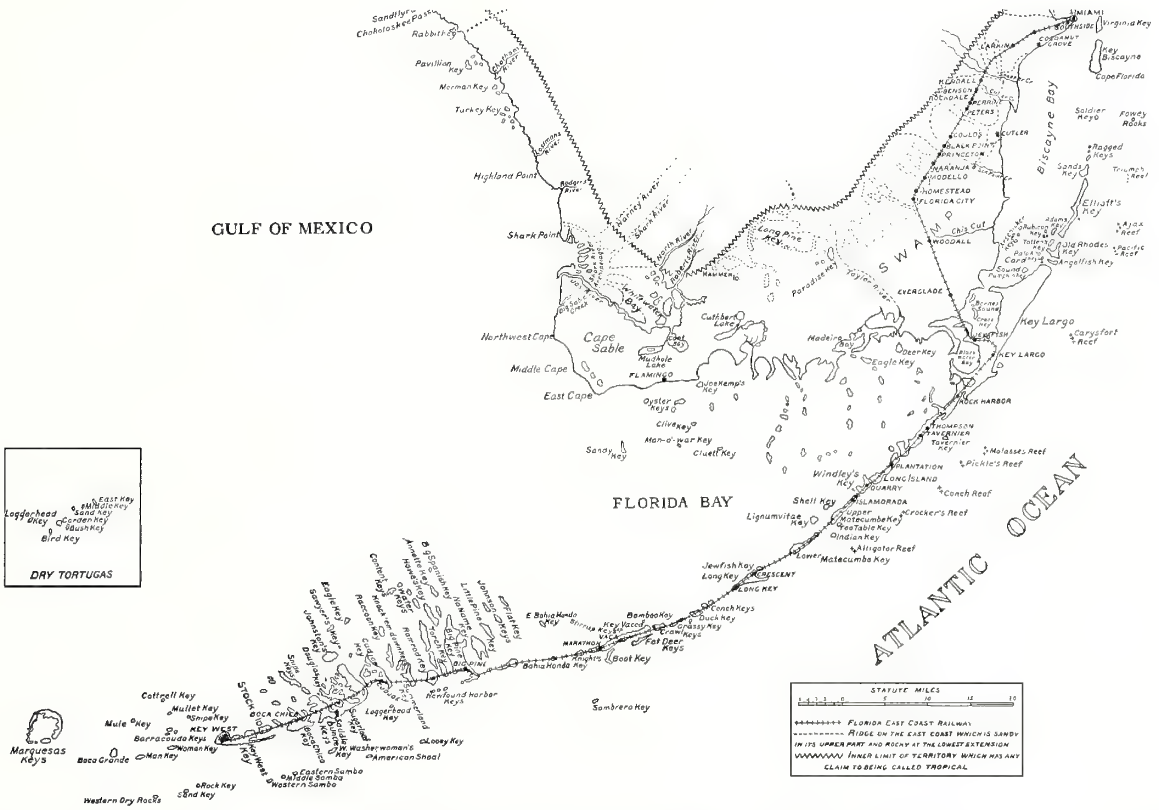
GULF OF MEXICO
Sandfly Pass
Chokoloskee Pass
Rabbit Key
Pavillion Key
Chatham River
Mormon Key
Turkey Key
Lostmans River
Highland Point
Rodgers River
Harney River
Shark River
Shark Point
North River
Roberts River
Shark River Archipelago
Joe River
Big Sable Creek
Whitewater Bay
HAMMER
Long Pine Key
Paradise Key
Taylor River
Cuthbert Lake
Coot Bay
Northwest Cape
Cape Sable
Mudhole Lake
Middle Cape
FLAMINGO
East Cape
Joe Kemp's Key
Oyster Keys
Clive Key
Man-o'-war Key
Sandy Key
Cluett Key
FLORIDA BAY
MIAMI
SOUTHSIDE
Virginia Key
COCOANUT GROVE
LARKIN
Key Biscayne
Cape Florida
KENDALL
BENSON
ROCKDALE
PERRINE
PETERS
Cutler Cr.
GOULDS
CUTLER
BLACK POINT
PRINCETON
NARANJA
MODELLO
Black Point Cr.
HOMESTEAD
FLORIDA CITY
Biscayne Bay
Soldier Key
Fowey Rocks
Ragged Keys
Sands Key
Triumph Reef
Elliott's Key
Adams Key
Rubicon Key
Totten Key
Old Rhodes Key
Ajax Reef
Pacific Reef
Palo Alto Key
Card Sound
Angelfish Key
Pumpkin Key
Chis Cut
WOODALL
SWAMP
EVERGLADE
Barnes Sound
Cross Key
Key Largo
Carysfort Reef
Madeira Bay
JEWFISH
Deer Key
Eagle Key
Black Water Bay
KEY LARGO
ROCK HARBOR
THOMPSON
TAVERNIER
Tavernier Key
Molasses Reef
Pickle's Reef
PLANTATION
Windley's Key
LONG ISLAND
QUARRY
Conch Reef
Shell Key
ISLAMORADA
Lignumvitae Key
Upper Matecumbe Key
Crocker's Reef
Tea Table Key
Indian Key
Alligator Reef
Lower Matecumbe Key
Jewfish Key
Long Key
CRESCENT
LONG KEY
Conch Keys
Duck Key
Grassy Key
Crawl Keys
Bamboo Key
Key Vaccas
VACA
MARATHON
Fat Deer Keys
Knight's Key
Boot Key
Stirrup Keys
E Bahia Honda Key
Bahia Honda Key
BIG PINE
Sombrero Key
ATLANTIC OCEAN
Loggerhead Key
East Key
Middle Key
Sand Key
Garden Key
Bush Key
Bird Key
DRY TORTUGAS
Spanish Key
Annette Key
Howe's Key
Content Keys
Water Keys
Little Pine
No Name Key
Johnson Keys
Flat Key
Big Pine Key
Torch Key
Ramrod Key
Knock 'em down Key
Raccoon Key
Eagle Key
Sawyer's Key
Johnston's Key
Cudjoe Key
Douglas Key
Snipe Keys
Summerland Key
Newfound Harbor Keys
Loggerhead Key
Sugarloaf Key
Saddle Bunch Keys
Boca Chica Key
STOCK
BOCA CHICA
Cottrell Key
Mullet Key
Snipe Key
Mule Key
KEY WEST
Barracouda Keys
Woman Key
Key West
Man Key
Boca Grande
Marquesas Keys
W. Washerwoman's Key
American Shoal
Looey Key
Eastern Sambo
Middle Sambo
Western Sambo
Rock Key
Sand Key
Western Dry Rocks
STATUTE MILES
5 4 3 2 1 0 5 10 15 20
FLORIDA EAST COAST RAILWAY
RIDGE ON THE EAST COAST WHICH IS SANDY IN ITS UPPER PART AND ROCKY AT THE LOWEST EXTENSION
INNER LIMIT OF TERRITORY WHICH HAS ANY CLAIM TO BEING CALLED TROPICAL

Fig. 2. Map of the Florida Keys, showing conditions after completion of the Florida East Coast Railway extension to Key West in 1912 (modified from Simpson, 1929).

later donated to the USNM. Much of Henderson's *Eolis* material has been subsequently sorted, identified (at least to family level), and distributed throughout the USNM mollusc collection. No comprehensive species lists were ever compiled, although nearly every systematic work on western Atlantic molluscs published since that time has included *Eolis* material (e. g., Pérez Farfante, 1945; Abbott, 1951; Boss and Merrill, 1965; Stuardo, 1982; Bieler and Mikkelsen, 1988; Salas and Gofas, 1997). Many specimens became type material of species described by Henderson's contemporaries (e. g., Dall, 1927; Simpson, 1920, 1929; Bartsch, 1934, 1940, 1943, 1947) and by Henderson himself (1920a).

The Smithsonian Station List

Because published cruise accounts do not exist, authors have relied on label information of individual lots in the Smithsonian (USNM/NMNH) collections, and on various (undated) versions of typed numbered station lists in the NMNH mollusc library, entitled "Marine Stations, *Eolis* collecting" (for a revised list, with corrections as per this paper, see the AMB web site cited above). Dated log entries throughout this paper refer to Henderson (1910-12) and Henderson (1912-16) in the Literature Cited section. These valuable lists begin with station 1 in Key West, 1910, and end with station 511 in Barbados, 1918. As part of their own research program on Florida Keys molluscs, the present authors tried to plot these *Eolis* stations on charts of Floridian waters to reconstruct Henderson's original collecting sites and routes. However, it quickly became obvious that the station numbers from the collection labels and USNM list do not reflect chronological order. For instance, there is no evidence that the *Eolis* (or Henderson) collected in Cuba during 1910; stations 16 and 17 apparently refer to material given to the Smithsonian during 1910, but resulted from Henderson's collecting in Cuba during 1908-09 (see Henderson's "Cuba" manuscript [not dated]). As another example, station 46 (1911) of the Smithsonian list is in Jamaica, but no mention is made of Jamaica in the 1911 *Eolis* log (Henderson did collect in Jamaica at other times: Simpson [1894] described a joint collecting trip in 1893). In addition, different sources (e.g., different specimen labels, and even different pages of the same publication by Henderson [1920a]) have disagreed on location or water depth. In some cases only retracing the actual cruise route will pinpoint the location of like-named islands such as

"Sand Key" or "Bird Key" that appear in multiple locations in the region. The following narrative provides such a reconstruction of events.

The Original Ship's Logs

To improve the accuracy of the *Eolis* stations listings and to solve questions concerning actual routes taken, we located and consulted Henderson's original handwritten cruise logs, now preserved in the Smithsonian Institution Archives and the National Museum of Natural History's Division of Mollusks (Henderson, 1910-12, 1912-16, 1918,[3] 1920d, and undated; see the NMNH and AMB web sites cited above for a summary account of these logs). From these, Henderson's collecting activities and the annual route of the *Eolis* were reconstructed for the years 1910 through 1916 (with some additional data for Henderson's activities in 1917 and 1918), although many unresolved questions remain. Henderson's narratives are a blend of technical ship's log and personal diary. One learns, for instance, about trying bouts of sunburn and mosquitoes, as well as his fondness for guanábana-flavored ice cream. Regrettably absent is a detailed list of samples collected. Stations are not numbered in the log even though various hauls are described, but it is not always clear which were successful (although "water haul" and "empty" are often noted). No original charts have been located, but were obviously used during the operations (the log remarks about discrepancies between expected and sounded depths during the dredging operations and at one point several charts were found missing — log entry of 1 May 1910). Nevertheless, Henderson's log books allowed us to reconstruct the major cruise events and locations, and provided a remarkable glimpse into the challenging conditions of collecting expeditions in the early 20th century.

Participants and Cruise Goals

Participants in Henderson's cruises illustrate well his academic connections. He was accompanied on most of his southern cruises by George Hubbard Clapp (1859-1949; Honorary Curator of Conchology at the Carnegie Museum, Pittsburgh, Pennsylvania) and Charles Torrey Simpson (1846-1932; USNM conchologist and botanist, later of Miami). Paul Bartsch (1871-1960; USNM Curator of Mollusks) participated in the 1912 and 1916 cruises. Bartsch brought to the cruises an association with the Tortugas Marine Biological Laboratory of the Carnegie Institution of Washington on Loggerhead Key, along with its scientists (Dr. Alfred Goldsborough Mayer, the Director [1868-1922; jellyfish researcher]; Dr. Thomas Wayland Vaughan of the U. S. Geological Survey [1870-1952; coral biologist; later of Scripps Institute for Biological Research, La Jolla, California]; Mr. G. Harold Drew, an Englishman from Cambridge University [studying marine bacteria]; and "Mr. Longley" [studying turtle development]) and research vessel, the *Anton Dohrn* with its launch, *Velella*. Others mentioned in the cruise logs include an ichthyologist, Mr. Louis L. Mowbray (listed as "from Boston," and later, the New York Aquarium) who visited in 1913 and 1915, and "Miss [Mary Jane] Rathbun" (1860-1943; USNM carcinologist) for whom crustaceans were frequently collected. The Assistant Light Keeper of the Garden Key Lighthouse is mentioned as collecting for Henderson (*Eolis* log entry, 11 June 1911). The Coast Guard Steamer *Bache* was visited while in dock due to weather in Key West, 4 June 1911. The 1914 Cuban cruise on the 65-foot fishing schooner *Tomas Barrera* included eminent Cuban malacologist Carlos de la Torre, and (as usual) Clapp, Bartsch, and Simpson, plus George W. Gill (USNM preparator), Manuel Lesmes (Havana Inspector of Fish), and Victor J. Rodríguez (University of Havana museum assistant).

Henderson was quite obviously a shell collector, first and foremost. He repeatedly expressed interest in finding and excitement in collecting a select list of relatively large-shelled gastropod species, namely *Cypraea exanthema* Linné, 1767 (= *C. zebra* Linné, 1758), *Voluta junonia* Lamarck, 1804 (now *Scaphella*), and *Voluta dohrni* Sowerby, 1903 (now *Scaphella*). His log of 14 June 1911 specifically cited the objective of the day's work as "to make another try for a *Junonia*." Dredge hauls without these key species were deemed failures or, at minimum, disappointments. All else was decidedly considered incidental; beach drift of micromolluscs and leaf litter with land snails were called "rubbish" and other materials in the dredge were "the usual wretched results." Searching for land snails, especially with Clapp and Simpson on board, was the ready alternative whenever weather or sea state prevented offshore work. Empty land shells were called "bones" and mention is made several times of Bartsch's experimental colonies of *Cerion* snails planted on various Keys (e. g., Bartsch, 1913, 1914).

The *Eolis* log entry of 11 April 1910 states: "It is our intention to explore with the dredge the Pourtalés Plateau and the reef lying off Hawk Channel and such shore collecting as may offer en route." The Pourtalés Plateau, a rocky, sloping area, 90-140 fms (165-255 m) deep off the Middle and Lower Keys, was a frequent objective, often confounded by swift currents of the Florida Current (the Florida Straits portion of the Gulf Stream) and the difficulties of deep-water hard-bottom sampling. But Henderson's resolve to risk such sampling was evident: "we might just as well lose the dredge and have done with it" (*Eolis* log entry, en route to Pourtalés Plateau, 31 May 1916).

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[3] With undated typed listing of station records; see also Henderson (1920b, c)

Collecting Gear

We have not located a detailed description of the collecting gear, but the *Eolis* apparently used a variety of tools. Over time, Henderson's logs refer to a pole dredge (employed from the side of the ship or its launch), a hand dredge (towed by hand from behind the launch), a "medium dredge" (considered too light in waters deeper than 70 fms in the conditions of the Pourtalés Plateau), a "large dredge" or "heavy dredge" (perhaps that referred to as "old Samson," lost on 10 June 1911; Henderson, 1911b),[4] and a beam trawl ("copied from *Blake* Report" *Eolis* log entry, 26 July 1910). In addition, baited traps were set, although rarely recovered. The ship's engineer (and later skipper) Greenlaw continuously modified and improved the dredging gear, and the 1915 cruise began with "several new dredges." Also during the 1915 cruise, the *Eolis* crew experimented with a diving apparatus "along a wire rope"; this may have been a hard-hat sponge diving outfit such as those used by Greek sponge divers in Florida during that time. Henderson abandoned the dive suit idea because of "pressure in ears too painful to stand" in 15 feet (*Eolis* log entry, 28 May 1915). Snorkeling gear was not evident, although "water buckets" (glass-bottomed to view the substratum?) or "water glasses" (*Eolis* log, 1913 and 1915 cruises) were used while wading on reefs at high tide. The logs do not give details of the preservation equipment and supplies available on board during the Keys cruises, but they were likely very similar to those used during the 1914 Cuba cruise on the *Tomas Barrera*: "There were four large copper tanks of alcohol of varying strengths, formalin, copper sulphate for 'doping' the tide pools, the various narcotizing reagents for expanding and killing specimens requiring such treatment, apparatus for injecting vertebrates, an amazing quantity of wide-mouth bottles and jars, instruments for oceanographic work, and many articles of special use to collectors and preparators, all of which had been selected with great care by Dr. Bartsch" (Henderson, 1916:7).

The Weather and Other Obstacles

Henderson chose the months of April and May for his annual cruises in the Florida Keys. Although the summer months would have likely offered calmer sea conditions, the tropical heat in days before air conditioning would have been unbearable at such times. Year after year, he seemed to have particularly bad luck with the prevailing conditions and several trips were cut short by foul weather. In 1910, weather caused Henderson to abandon plans for the Dry Tortugas and the rest of the cruise; in 1912, foul weather cut dredging short in the Bahamas; in 1913, the conditions left Henderson "disgusted and dejected"; in 1915, the cruise is abandoned because of continued "wretched conditions"; and in 1916, Simpson departed early because of poor weather (although that cruise eventually culminated in "fine day with glorious results"; *Eolis* log entry, 4 June 1916). Stormy seas made it unpleasant to travel (the heavy chop of 30 May 1915 smashed all plates on board, reflected by Henderson's note of a "heavy toll in crockery"), but more importantly cancelled all hope of dredging. When the weather was particularly poor, Clapp and Henderson repeatedly considered abandoning the *Eolis* cruise and to take a ship from Key West to Cuba "to try out the landshelling there" (*Eolis* log entry, 26 May 1911). Each cruise invariably began with great plans and high hopes - and, regardless of the ultimate outcome in collected specimens, usually ended with a disappointed Henderson who had expected more. The fourth annual cruise, for example, ended "with results far below the standard set by our first one" and realization that "*Eolis* [is] too small a craft for this purpose" (*Eolis* log entry, 23 May 1913); the 1915 cruise was in turn described with "results far below the average" (*Eolis* log entry, 2 June 1915).

The tropical heat was a frequent topic of Henderson's log entries: "terrifyingly hot - one wears nothing but the thinnest pajamas" (*Eolis* log entry, 17 April 1910). The 1911 cruise, at a slightly later time extending into June, brought painful sunburns, which Henderson treated (on advice of Dr. Mayer) with picric acid.[5] The discomfort caused by the high temperatures and burning sun was only exceeded by the mosquitoes ("The boat below is simply swarming with mosquitoes. Such a night of horror!"; *Eolis* log entry, 23 June 1911) and red bugs (chiggers), which were combated by lighting citronella and taking kerosene baths, respectively. The high temperatures encountered during the spring months (e. g., 94ºF [34ºC] in the cabin; *Eolis* log entry, 26 May 1915) likely discouraged him from any attempt at summer work in the Keys with his vessel. Post-summer cruising dates, during the fall hurricane season, were also out of the question: the hurricanes of 1910 and 1911 wrecked havoc in Key West (Browne, 1912) and must have negated any such plans.

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[4] The "June 11" entry is not part of the original log and was added for this article by Henderson to reflect the discovery of the a specimen of the rare *Haliotis pourtalesii* in "a haul made yesterday"; the specimen was dredged on May 31. Foster (1946), in the redescription and neotype designation of *H. pourtalesii* (pp. 38-39) claimed this was collected in 1913. This probably results from Henderson's statement, published in 1915 (p. 659), that he dredged the specimen "Two years ago." However, in the synonymy on the following page (1915: 660), Henderson explicitly referred to the 1911 rediscovery.

[5] This was a somewhat unconventional treatment — picric acid, also known as trinitrophenol, is employed as a component in histological preservation fluids (e. g., Bouin's Fixative) or as a military explosive that is used as a booster charge to set off another less sensitive explosive, such as TNT. Among the lesser effects of exposure, the U.S. Occupational Safety and Health Guidelines mention skin and eye irritation, allergic skin rash, and yellow staining to skin and hair. Henderson indeed remained "yellow for a week or so" (*Eolis* log entry, 8 June 1911).

Weather and blood-sucking insects were not the only obstacles encountered during these relatively short cruises. Today's ease of cruising the well-charted waters of the Keys in reliable motor-powered crafts gives little indication of the challenges faced by Henderson and his vessel. Henderson's logs often show his exasperation with the mismatch of charted and sounded depth, and the vessel ran hard aground on numerous occasions (in fact, the 1910 maiden cruise began with a grounding when trying to leave Miami Harbor; the last day of the 1912 cruise and the first day of the 1913 cruise also found the *Eolis* hard aground at Miami). Work with the large dredge was not always successful - during one of the very first tries in deeper water, the *Eolis* dredge apparently snared the Havana telegraph cable (*Eolis* log entry, 22 April 1910); this dredge was hung up again and lost completely during the second cruise (*Eolis* log entry, 31 May 1911). Other disappointments included equipment failures (a gasoline leak in 1910, a ship's compass "considerably off the true" in 1911) and unexpected obstacles preventing the party from reaching localities in Florida Bay through certain cuts between the individual islands that form the Keys. While Henderson must have been prepared for the newly constructed bridges and viaducts of the Florida East Coast Railway's Key West extension (the first train reached Key West in 1912), he had not foreseen the numerous temporary wooden trestles that restricted vessel traffic across the island chain (Gallagher, 1995). Planned visits to bayside locations (e. g., Knight's Key dock [*Eolis* log entry, 16 April 1910] and Lignum Vitae Key [*Eolis* log entry, 11 May 1913]) were thus rendered impossible. Many of the sites visited by Henderson's party were traffic hubs and important docking facilities at the time, such as Knight's Key (the terminus of the Railway until 1912 and an important dock with regular commercial service), Pigeon Key (a work camp for the FEC Railway, 1908-12), the Long Key Fishing Camp, and of course Key West, which in the late 19th century had developed into the largest and richest city in Florida.

Collecting and Processing of Samples

On good collecting days, Henderson was faced with the challenges known to all biological expeditions: "The danger threatening us is a plethora of specimens and a lack of time and inclination to properly clean them" (*Eolis* log entry, 13 April 1910). He showed dedication and efforts to catch up, often staying on board to take care of specimens while others continued collecting. Some material was alcohol-preserved (i. e., "alcohol[ing] today's catch," *Eolis* log entry, 18 April 1910); large shells were "boiled out" (*Eolis* log entry, 29 May 1911). Despite these efforts, the surviving logs and other records do not provide a detailed account of locality data and samples. A bag numbering system used by Henderson during the 1911 cruise was replaced without explanation by a tag numbering system once the collections were transferred to the Smithsonian Institution. Unfortunately, the resulting account indicates that many samples may have been combined or lost.

The Revised *Eolis* Station List

In this report, we have attempted to reconcile three sources of station data: (1) probable stations as gleaned from the chronological *Eolis* logs, (2) the Smithsonian "station" list (see web sites as cited above), already acknowledged as out of chronological order and containing extraneous material, and (3) station data as listed on selected specimen labels in the USNM collection (Henderson's material is now dispersed throughout the Smithsonian's vast collection; no attempt has been made to locate all specimens belonging to the *Eolis* cruises). In some cases, the log refers to numbered "bags," which can be matched to narrative descriptions. On the other hand, the Smithsonian "station" list originated in tags apparently assigned to samples as they were received and/or unpacked at the Smithsonian (Henderson's log occasionally mentions such trips to deposit specimens). Material from some stations described in the log (e.g., "hauls at 20 ft, just in between Pickles and Conch Reefs"; *Eolis* log entry, 15 April 1910) were either not retained or never deposited at USNM. Because the information in the Smithsonian "station" listings and the collection labels is often much more detailed than the log entries, we assume that Henderson or his captain (initially C. B. Mitchell [stricken with malaria following the 1911 cruise], later Sidney Greenlaw) improved upon the recorded station information through subsequent chart work.

In contrast to more conventional expedition station data (such as those issued by the U. S. Commissioner of Fisheries for the cruises of the *Albatross, Blake*, and other vessels; e.g., Townsend, 1901), it is apparent that the *Eolis* station numbers were created after the fact and reflect the sequential donation of Henderson's material to the Smithsonian. This is evident in the fact that some of the dates on the list (e.g., October, November) do not correspond to those of any of the spring cruises (mostly April and May). Henderson (or subsequent USNM collections staff) at least once combined several collecting stations during processing (e. g., two Lower Matecumbe Key collections of 15 May 1911, combined as "bag 16" by Henderson and further combined with an Indian Key sample as station 45 by USNM). Additionally, his captain and crew apparently collected before or after the spring cruises and this material was added to material sent to the museum, although these data were never recorded in Henderson's cruise logs (in a note published in February, Henderson [1914: 120] mentioned that "a few weeks ago the skipper of my little

Table 1. *Eolis* Collection Stations ("?" indicating some degree of uncertainty, either multiple possibilities from Smithsonian *Eolis* station list, or inexact match with *Eolis* log; ft = feet [0.3 m], fms = fathoms [6 ft], mi = mile [1 nautical mile = 1.85 km, sta. = station).

Date	Probable collection station (with corresponding bag number) according to *Eolis* log	Corresponding station from Smithsonian *Eolis* station list
11 April 1910	Biscayne Bay, trial dredge, 15 ft, sand	
13 April 1910	2 mi S by E of Fowey Rocks Light, 2 dredge hauls, 40-50 fms	?sta. 14, off Miami, 40 fms (this station alternatively described as Tavernier Key, tidal flats exposed to 2 ft, coralline and sand), 1910
13 April 1910	1 mi S by E of Fowey Rocks Light, 25 fms, coral sand detritus (material "bagged for future work")	sta. 8, off Fowey Light, 1 mi SE, 25 fms, coral detritus, sand, black shell, 1910
13 April 1910	Caesar's Bank, pole dredge, 7 ft at low tide	
13 April 1910	Elliot Key, soft sandy coral beach, shore collecting	
14 April 1910	Elliott Key banks, shore collecting	
14 April 1910	Unnamed "outer reef" (Upper Keys), dredge, sand	
14 April 1910	Mangrove island near Drago (= Rodriguez) Key, mangrove roots	
15 April 1910	inside outer reef between Pickles and Conch Reefs, 2 dredge hauls, 20 ft	
15 April 1910	outside outer reef between Pickles and Conch Reefs, dredge	?sta. 7, off Conch Reef, 2 mi off, 35 fms, coral sand, 1910
15 April 1910	Key Largo, near-shore collecting	
15 April 1910	Tavernier Key bank, at low tide	?sta. B, Tavernier (as "Tavenier") Key, 1910; OR sta. 14, off Miami, 40 fms (also given as Tavernier Key, tidal flats exposed to 2 ft, coralline and sand), 1910
17 April 1910	NE corner Bahia Honda Key, "shelling bank"	?sta. D, Bahia Honda Key, shore station (drift), 1910
18 April 1910	Loue (= Looe) Key, hand-collected, low tide	sta. I, Loue Key Reef, "a mere patch of coral covered sand in outer reef," coral blocks at low tide, 1910
19 April 1910	off Key West, 3 mi out from reef, 1 haul, "slightly shallower [than 65 fms]," sand	?sta. 1, off Key West, 3 miles SSE of Channel Buoy, 55 fms, sand, 1910; OR sta. 5, off Key West, 3.5 mi SSE of Channel Buoy, 60 fms, sand (and shells), 1910 (OR 26 April 1910)
19 April 1910	off Key West, Pourtales Plateau, 5-6 mi out from reef, 1 haul, 100 fms, rocky	sta. 15, Sand Key, 5 mi S, 100 fms, sand and coral fragments, Gulf Stream, 1910
19 April 1910	off Sand Key, several hauls, 25-35 fms, sand/broken coral	?sta. 2, off Sand Key, SW of Light, 27-3) *[sic]* fms, broken coral detritus, 1910; OR sta. 6, off Sand Key, SE of Light, 35 fms, (coral) sand and broken shells, 1910
20 April 1910	Key West, south beach, shore collecting	sta. G, Key West, beach on S side near Old Fort and Slaughter House, 1910
21 April 1910	off Key West, out channel S by W, 1 haul, 69 fms	sta. 3, off Sand Key, SW of Light, 69 fms, sand broken shell (?or as "off Key West, 63 fms"; Henderson, 1920a: 80), 1910
21 April 1910	off Key West, out channel S by W, 1 haul, 80-90 fms	?sta. 12, off Sand Key, SW of Light, 80 fms, hard sand and coral fragments, 1910
22 April 1910	8 mi off Sand Key Light, N by W, Pourtales Plateau, large dredge, 130 fms, rocky	?sta. L, off Sand Key, about 10 mi S (also given as S to SE), Pourtales Plateau, 125 fms, rocky, 1910
22 April 1910	off Sand Key, 1 haul, 6 or 8 fms, sand	
22 April 1910	Sand Key, reef collecting	?sta. F, Sand Key Reef, shore station at low tide, blocks of dead coral, 1910
23 April 1910	off Cape Sable, short dredge hauls, 10 ft, broken shell/coral	sta. 4, off East Cape Sable, 1 mi off, 1.5 fms (?or as 10 ft), coralline, 1910
24 April 1910	Cape Sable, beach collecting	
26 April 1910	off Key West, Hawk Channel, dredge	sta. A, Hawk Channel, Florida, 1910
26 April 1910	off Key West, 3 miles out, 60 fms, 2 hauls (2nd haul is Key West bearing NW by N / N, and Sand Key Light, W 1/2 N)	?sta. H, Sand Key, 60-65 fms, sand, 1910; OR sta. 5, off Key West, 3.5 mi SSE of Channel Buoy, 60 fms, sand (also given as sand and shells), 1910 (OR 19 April 1910)

(Table 1 continued)

Table 1. (Continued)

Date	Probable collection station (with corresponding bag number) according to *Eolis* log	Corresponding station from Smithsonian *Eolis* station list
6 May 1910	Fernandina Beach, shore collecting	
22 May 1911	N side of Caesar's Creek Bank, pole dredge, 8 ft	
22 May 1911	N of Caesar's Creek Bank, 3 hauls with trawl, 10 ft (information for bags 13, 14, 15 given as "Caesar's Bank N, 9 ft")	sta. 40, Hawk Channel, just N of Caesar's Creek Bank, Florida, 10 fms (Henderson, 1920a: 46; or 10 feet), 1911
23 May 1911	Caesar's Creek, mangroves	
23 May 1911	Caesar's Creek between Elliott and Rhodes Keys, shallow water	
23 May 1911	N side Caesar's Creek, old coral reef	
23 May 1911	Rodriguez Key, shore collecting	
24 May 1911	Key Largo, drift (information for bag 9 given as Key Largo drift; bag 11, Key Largo opposite Rodriguez Key)	
24 May 1911	Tavernier Key, center, shore drift collecting (information for bags 7, 8 given as Tavernier Key drift; bag 10, Key Largo "rubbish" off Tavernier)	
24 May 1911	Indian Key, S side, shore collecting	
25 May 1911	Indian Key, shore collecting, low tide	
25 May 1911	Lower Matecumbe Key, shore collecting (this and the following combined as bag 16 = Lower Matecumbe "sand rubbish" and marl marines)	sta. 45, Lower Matecumbe (and Indian) Key, shore drift, 1911; combining all logged collections of that day
25 May 1911	Lower Matecumbe Key, marine marl along railroad track, dredged from bayside of west end of Upper Matecumbe Key	
?? May 1911	"only one haul has been made ... within Hawks Channel" (date uncertain)	
28 May 1911	off Key West, 3 mi S of channel buoy, several hauls, medium dredge and trawl, 63 fms, fine coral sand (bags 19, 20, 21 are from, off Key West, 60 fms)	sta. 42, off Key West, 60 fms, 1911
28 May 1911	off Key West, 4 mi S of channel buoy, 1 haul, medium dredge, 80 fms, coarse bottom (bags 22, 23 are from off Key West, 80 fms)	
28 May 1911	Sand Key Reef, reef collecting (bag 17 contains *Turbo* from Sand Key Reef; bag 18, also from Sand Key)	sta. 37, Sand Key Reef, shore station among coral blocks at low tide, 1911
30 May 1911	Key West bearing NW by N / N, and Sand Key Light, W 1/2 N; large dredge, 50 fms (bag 24 is from SE of Key West, 50 fms)	?sta. 44, off Key West, 50 fms, sand, 1911
30 May 1911	off Key West, edge of Pourtales Plateau, large dredge, 3 hauls, 90 fms, broken coral (bags 25, 26 are from SE of Key West, 90 fms; bag 27 with *Haliotis* from SE of Key West, 90 fms)	sta. 31, off Sand Key (?or as off Key West; Henderson, 1920a: 112) 90 fms, sand, 1911
30 May 1911	SW of Key West, 100 fms, 2 hauls, coarse coral sand	
30 May 1911	Key West, beach collecting near railroad	?sta. 35, Key West, N side of beach, shore station, 1911 (OR 6 June 1911)
31 May 1911	Pourtales Plateau, 50 min past Sand Key, S by W, 7 mi and outer buoy from Sand Key Light, N = "no. 2" from outer buoy to inner NE by N = "no. 1" (1st haul 116-120 fms; 2nd haul "somewhat deeper")	
1 June 1911	off Sand Key, 2 hauls with trawl and 1 with medium dredge, 61 fms, shelly (bags 28, 29, 30 are from off Sand Key, due S, 61 fms)	?sta. 32, Tortugas, 16 fms (?or off Sand Key, 61 fms), sand, 1911 (OR 8 June 1911)
1 June 1911	off Sand Key, shallower by a few fms [than 61 fms], 1 haul, soft bottom	

(Table 1 continued)

Table 1. (Continued)

Date	Probable collection station (with corresponding bag number) according to *Eolis* log	Corresponding station from Smithsonian *Eolis* station list
1 June 1911	off Sand Key, nearer lighthouse, 1 haul	
1 June 1911	off Sand Key, 1.5 mi from lighthouse, 31 fms	
1 June 1911	off Sand Key, 1 haul, 60 fms, soft bottom	
2 June 1911	due S of Sand Key, 5 hauls, 60, 65, 70 fms, soft or coarse sand (bags 31-36 are from off Sand Key, 63 fms)	sta. 43, off Key West, 63 fms, sand, 1911
3 June 1911	Key West, 3 mi W from bell buoy of NW Channel, several trawl hauls, 4.5 fms, "hard" on chart	?sta. 71, off Key West (reef) (?or as Hawk Channel, off East Martello Tower), 4.5 fms, 1913
3 June 1911	Key West, 3 mi NW from previous station, 6.5 fms, "hard" on chart (bag 37 is from 5 mi NW of entrance to Key West, Gulf of Mexico, 6.5 fms, hard to soft bottom)	sta. 30, off Key West, 5 mi off N entrance to Key West Channel, 7 fms, sand, 1911
6 June 1911	Key West, near East Martello Tower, shore collecting	?sta. 35, Key West, N side of beach, shore station, 1911 (OR 30 May 1911)
6 June 1911	Key West, S of East Martello Tower, haul at red buoy number 4	
6 June 1911	Key West, S of East Martello Tower, past reef at buoy number 2, 10 fms, hard rocky bottom	
6 June 1911	Key West, S of East Martello Tower, several hauls, 20 fms	?sta. 39, off Key West, 1 mi SE of Buoy no. 2, 20-25 fms, 1911
8 June 1911	Dry Tortugas, Garden Key, mote at Fort Jefferson	
8 June 1911	Dry Tortugas, 2 mi SE of Fort Jefferson, 3-4 hauls with trawl, hard "bubbly" bottom (bag 38 is from Tortugas, 16 fms)	?sta. 32, Tortugas, 16 fms (?or off Sand Key, 61 fms, sand, 1911) (OR 1 June 1911); OR sta. 33, off Dry Tortugas, E, southwest channel, 16 fms, 1911
8 June 1911	Dry Tortugas, at reef, hand-collecting	
9 June 1911	Dry Tortugas, Garden Key, 3 mi out from red sea buoy, 5 dredge hauls, 14-15 fms, hard sand	sta. 34, off Dry Tortugas, E, 15 fms, 1911
9 June 1911	Dry Tortugas, Garden Key, mote at Fort Jefferson, wading	
9 June 1911	Dry Tortugas, Garden Key rock reef, "neck deep" (bag 39 is from Dry Tortugas, Garden Key, shore drift)	sta. 41, Dry Tortugas, Garden Key, beach drift, 1911
10 June 1911	Dry Tortugas, Garden Key, 3 mi SE from red sea buoy, dredge	
10 June 1911	Dry Tortugas, Garden Key, 2 mi E of previous station, dredge	
10 June 1911	Dry Tortugas, Garden Key, W side of mote at Fort Jefferson	
11 June 1911	Dry Tortugas, Garden Key, collections by assistant lightkeeper	
11 June 1911	Dry Tortugas, Garden Key rock reef, hand-collecting	
12 June 1911	Dry Tortugas, Garden Key, out SW channel, 4-5 dredge hauls, 5-11 fms (bags 40-43 are from Tortugas dredging)	?sta. 36, off Dry Tortugas (southwest channel entrance), 18m (10 fms), 1911
12 June 1911	Dry Tortugas, W side Garden Key, shovel & clam rake	
12 June 1911	Dry Tortugas, Garden Key, mote wall at Fort Jefferson, pile of coral rubble on shore	
13 June 1911	Dry Tortugas, Loggerhead Key, beach collecting	?sta. 367, off Loggerhead Key (north end), Dry Tortugas, arrived August 1917
14 June 1911	Dry Tortugas, off Garden Key, E and NE of red sea buoy number 2, 6 hauls, various types of bottom	
14 May 1912	Bahamas, North Bimini, intertidal	
15 May 1912	Bahamas, off little island at N end of North Bimini, dredge	?sta. 50, Bahamas, North Bimini Island, off N end in sand and rocky patches, 20 fms, 1912
16 May 1912	Bahamas, South Bimini, intertidal rocks and beach collecting	?sta. 72 and 74, Bahamas, South Bimini Island, shore drift, as 1912
17 May 1912	Bahamas, North Bimini, 6-8 hauls with dredge, various types of bottom	
17 May 1912	Bahamas, island S of South Bimini, tidepools	

(Table 1 continued)

Table 1. (Continued)

Date	Probable collection station (with corresponding bag number) according to *Eolis* log	Corresponding station from Smithsonian *Eolis* station list
18 May 1912	Bahamas, North Bimini, flats	
20 May 1912	Bahamas, North Bimini, beach collecting	
22 May 1912	Bahamas, South Cat Cay, Dollar Harbor, many dredges, 2-3 ft *[sic]*	?sta. 47, Bahamas, South Cat Cay, 1/4 mi off, 3 fms, sand with coral patches, 1912
23 May 1912	Bahamas, off North Cat Cay, hauls, 1-3 fms, various types of bottom	
24 May 1912	Bahamas, 70-72 ft	
24 May 1912	Bahamas, 3.5 fms	
27 May 1912	Miami, out New Cut, 3 hauls with trawl, 30 fms, coral detritus	
28 May 1912	Miami, out New Cut, 24 fms, grass/sand	sta. 51, off Miami, off New Cut, 24 fms, sand, 1912
28 May 1912	Miami, out New Cut, 42 fms, sand	
28 May 1912	Miami, out New Cut, 60 fms, 2 hauls, green mud	sta. 48, off Miami, off New Cut, 60 fms, sand (Henderson, 1920a: 25) or green mud (Henderson, 1920a: 26, 54, 79, 133); or light greenish mud, soft, 1912
28 May 1912	Miami, out New Cut, 30 and 35 fms	
29 May 1912	Fowey Rocks, coralline bank collecting	
29 May 1912	Fowey Rocks, dredge haul, 24 fms	
31 May 1912	Miami, out of New Cut, several hauls, 30 fms	?sta. 49, off Miami, off New Cut, 30 fms, sand and coral (or as sand, coral detritus; or as sand broken coral), 1912
31 May 1912	Miami, out of New Cut, several hauls, 20 fms	?sta. 62, off Miami, off New Cut, 20 fms, as 1913; OR sta. 103, off Miami, off New Cut, 20 fms, October 1914
5 May 1913	Ragged Keys, hand dredging, 9 ft	
6 May 1913	Ragged Keys, hand dredging & "work flats" at low tide	
7 May 1913	off Turtle Harbor, 1 mi out from red nun buoy on reef line, 20 fms (bags 1, 2 are from off Turtle Harbor, 20 fms)	sta. 59, off Turtle Harbor, 20 fms, 1913
7 May 1913	off Turtle Harbor, 1 mi out from red nun buoy on reef line, 40 fms (bags 3-5 are from off Turtle Harbor, 40 fms)	sta. 61, off Turtle Harbor, 40 fms, 1913
7 May 1913	off Turtle Harbor, 1 mi out from red nun buoy on reef line, 50 fms (bags 6-8 are from off Turtle Harbor, 60 fms)	sta. 58, off Turtle Harbor, 50 fms, 1913
8 May 1913	Old Rhodes Key, hand dredging	
9 May 1913	Ajax Reef, hand dredging	?sta.55, Florida reef, off Ajax Reef, inside of, 4 fms, 1913
10 May 1913	Ajax Reef, from baited traps	
10 May 1913	Tavernier Key, shore collecting, low tide	
11 May 1913	Tavernier Key, baited traps near mangroves	
11 May 1913	Upper Matecumbe Key, beach drift	sta. 60, Upper Matecumbe Key, shore drift, 1913
11 May 1913	[Indian Key, set baited traps]	?sta. M, Indian Key, shore drift, 1913
12 May 1913	Indian Key, baited traps	
15 May 1913	Key West, NW channel and westerly bank, hand dredging, hard bottom	?sta. 102, off Key West (Gulf), 9 fms (?or as 10 fms [Henderson, 1920a: 68]; ?or as less than 10 fms), October 1914
15 May 1913	Key West, due N in channel, 15-20 hand dredges (bags 9-10 are from Key West, inside, 3-20 ft)	sta. 65, off Key West, inside Hawk Channel, 3-20 ft, 1913
16 May 1913	off Key West, Hawk Channel, hand dredging (bag 11 is from	sta. 66, off Key West, 3-4 fms (?or as Hawk Channel, 25 ft; Henderson, Key West, Hawk Channel, 25 ft) 1920a: 46), 1913
18 May 1913	due S from Sand Key, 40 fms (bag 12 is from S of Sand Key, 40 fms)	sta. 57, off Sand Key, 40 fms, 1913
18 May 1913	due S from Sand Key, 50 fms	

(Table 1 continued)

Table 1. (Continued)

Date	**Probable collection station (with corresponding bag number) according to *Eolis* log**	**Corresponding station from Smithsonian *Eolis* station list**
18 May 1913	Sand Key, reef collecting, low tide	
19 May 1913	3/4 mi off Sand Key, patch reef, 2 dredge hauls, 30 ft	?sta. 73, off Key West, just inside reef, 5 fms, broken coral, sand, 1913; OR sta. 75, off Key West, inside channel buoy on reef, 5 fms, 1913
19 May 1913	off Sand Key, 1 haul, 20 fms, sand	
19 May 1913	off Sand Key, 1 haul, 52 fms	
19 May 1913	off Sand Key, 2 hauls, 70 fms (noting 2 dead *Voluta dohrni*)	?sta. 56, off Sand Key, 70 fms, sand, 1913; OR ?sta. 63, off Key West, 143 m (78 fms), small rocky fragments, Gulf Stream, "[*Voluta*] *dohrni*", 1913 (OR station below)
19 May 1913	off Sand Key, edge of Pourtales Plateau, 82 fms, hard bottom (noting *Voluta dohrni*)	?sta. 63, off Key West, 143 m (78 fms), small rocky fragments, Gulf Stream, , "[*Voluta*] *dohrni*", 1913 (OR station above)
19 May 1913	Eastern Dry Rocks, reef collecting, low tide (several unnumbered bags)	
22 May 1915	off Sand Key, heavy dredge, 58 fms, fine sand	sta. 159, off Sand Key, SW, 58 fms, sand, 1915
22 May 1915	Sand Key, reef collecting, high tide	
23 May 1915	out ship channel SE of Key West, 1 haul, 62 fms, sand	sta. 160, off Sand Key, 62 fms, sand, 1915
23 May 1915	out ship channel SE of Key West, into Gulf Stream, 1 haul, 70 fms, coarse sand	
23 May 1915	out ship channel SE of Key West, into Gulf Stream, 1 haul, 80 fms, coarse sand	
24 May 1915	Middle Sambo Reef, reef collecting	
24 May 1915	off Middle Sambo Reef, 1 haul, 10 fms, soft coral mud	
24 May 1915	off Middle Sambo Reef, several hauls, "deeper" [than 10 fms]	?sta. 195, off Sambo Reef, 50 fms, sand, 1915 AND/OR sta. 196, off Sambo Reef, 58 fms, sand, 1915
24 May 1915	off Middle Sambo Reef, with land out of sight, 1 haul, 80-90 fms	?sta. 197, off Sambo Reef, 75 fms, 1915
25 May 1915	SW of Sand Key, 1 haul, 76 fms, sand/mud	sta. 161, off Sand Key, 139 m (76 fms), sand, 1915
25 May 1915	SW of Sand Key, 1 haul, 85 fms, sand	sta. 163, off Sand Key, 155 m (85 fms), 1915
25 May 1915	SW of Sand Key, Pourtales Plateau, 1 haul, 95 fms, coarse sand	sta. 301, off Sand Key, 95 fms, rocky, 1915
25 May 1915	due SE of Sand Key Light, 1 dredge haul (15 min.), 100 fms, fine sand	sta. 302, off Sand Key, 100 fms, 1915
26 May 1915	due S of Key West, 1 haul, 92 fms, coarse sand	sta. 164, off Sand Key, 92 fms, 1915
26 May 1915	due S of Key West, 1 haul, 100 fms	
26 May 1915	SE of Key West wireless tower, American Shoals in sight, dredge, 98 fms	sta. 146, off Key West, 98 fms, 1915
27 May 1915	Key West, breakwater at outer end of NW channel, few hauls	
27 May 1915	Key West bell buoy, 1 haul	
28 May 1915	Sand Key, reef collecting, low tide	
30 May 1915	Boca Grande Key, shore collecting	
31 May 1915	Boca Grande Key, flats collecting, low tide, calcareous mud	
1 June 1915	Boca Grande Key channel, several dredge hauls, rocky	
1 June 1915	Boca Grande Key channel, several dredge hauls, sand/weedy	
1 June 1915	Boca Grande Key channel, dredge, seafan fields	
June 1915	Captain to continue dredging, off Indian Key and Fowey Rocks, en route to Miami	
24 May 1916	due S of Key West, 1 haul, 90 fms	sta. 334, off Key West, 90 fms, 1916

(Table 1 continued)

Table 1. (Continued)

Date	Probable collection station (with corresponding bag number) according to *Eolis* log	Corresponding station from Smithsonian *Eolis* station list
24 May 1916	due S of Key West, 1 haul, 100 fms, sand	?sta. 324, off Sand Key, NW 1/2W, 100 fms, 1916; or sta. 344, off Key West, 100 fms 1916
24 May 1916	Key West bearing NNW, 110 fms, 1 haul, coarse sand	sta. 333, off Key West, 110 fms, 1916
24 May 1916	Middle Sambo Reef, wading, high tide	
27 May 1916	due S of Western Dry Rocks beacon, 1 haul, 25 fms, stones/algae	sta. 345, off Key West, 25 fms, 1916
27 May 1916	off Western Dry Rocks beacon, 1 haul, 65 fms, rough bottom	sta. 321, off Western Dry Rocks, 119 m (65 fms), 1916
27 May 1916	off Western Dry Rocks beacon, 1 haul, 80 fms, fine sand/stones	?sta. 320, off Western Dry Rocks, 146 m; 80 fms (?or off Sambo Reef, 120 fms), arrived August 1916
27 May 1916	off Western Dry Rocks beacon, Pourtales Plateau, 1 haul, 90 fms, rocky	sta. 319, off Western Dry Rocks, 165 m (90 fms), arrived August 1916
27 May 1916	Sand Key, reef collecting	
29 May 1916	Marquesas Keys, bank collecting	
30 May 1916	Sand Key NW 1/2 N and Key West N 1/2 E, 1 haul, 75 fms, soft coarse sand	?sta. 314, off Key West, 75 fms, arrived August 1916; OR sta. 326, off Sand Key, SE by E, 75 fms, 1916
30 May 1916	Sand Key NW 1/2 N and Key West N 1/2 E, 1 haul (35 min.), 87 fms, sand	sta. 315, off Key West, 87 fms, 1916, arrived August 1916
30 May 1916	just inside Sand Key reef, several hauls, 10-20 fms, soft mud	?sta. 313, off Key West, 16 fms (?or as 10 fms), arrived August 1916
31 May 1916	W of Sand Key, bearing NE by N 1/2 N, 95 fms, coarse sand	?sta. 318, off Western Dry Rocks, NE by N 1/4 N, 95 fms, arrived August 1916; OR sta. 325, off Sand Key, ESE, 174 m (95 fms), arrived August 1916
31 May 1916	Pourtales Plateau, Sand Key Light and Key West wireless towers in line, 1 dredge haul (45 min.), 120 fms	
31 May 1916	off Sand Key, Pourtales Plateau, 2 dredge hauls (1st 35 min.), 144 fms	sta. 341, off Western Dry Rocks, 144 fms, arrived August 1916
31 May 1916	10 mi off Sand Key reef, 120 fms, smooth sand/rocks	sta. 316, off Sand Key, 120 fms, arrived August 1916
4 June 1916	Sand Key Light bearing NW by W 1/2 W, ~15 mi S of Sambo Reef Key, KW wireless towers visible, 2 dredge hauls (1st 30 min.), 110 fms (labeled bags "Sambo")	?sta. 323, off Sand Key, NW by W, 110 fms, 1916; OR sta. 343, off Sambo Reef, 110 fms, 1916
4 June 1916	Sand Key Light bearing NW by W 1/2 W, ~15 mi, about S of Sambo Reef Key, KW wireless towers visible, 1 haul (30 min.), 120 fms, stones	sta. 330, off Sambo Reef, 219 m (120 fms), 1916, arrived August 1916
4 June 1916	Sand Key Light bearing NW by W 1/2 W, ~15 mi, about S of Sambo Reef Key, KW wireless towers visible, 1 haul, 115 fms, sand/rocks	sta. 332, off Sambo Reef, 115 fms, arrived August 1916
4 June 1916	Sand Key Light bearing NW by W 1/2 W, ~15 mi, about S of Sambo Reef Key, KW wireless towers visible, 1 haul, 118 fms, pebbles	sta. 331, off Sambo Reef, 118 fms, arrived August 1916
4 June 1916	Sand Key Light bearing NW by W 1/2 W, ~15 mi, about S of Sambo Reef Key, KW wireless towers visible, 1 haul, 135 fms, sand/rubble	sta. 329, off Sambo Reef, 135 fms, arrived August 1916
5-23 June 1916	Key West, captain continues dredging while Henderson in Cuba Example: 23 June, 85-110 fms, light large dredge	

Table 2. Coordinates for landmarks cited in Henderson's *Eolis* log descriptions.

Location (in alphabetical order)	**Latitude (degrees and minutes North)**	**Longitude (degrees and minutes West)**	**Comment (exact location, referring to current waypoints)**
Ajax Reef	25°24.0'	080°08.0'	
Alligator Reef (Lighthouse)	24°51.103'	080°37.134'	
American Shoal (Lighthouse)	24°31.507'	081°31.169'	
Bahia Honda Key (NE corner of)	24°40.53'	081°15.07'	red nun buoy no. 2
Bird Key (center of)	24°37.32'	082°53.13'	
Boca Grande Key (center of)	24°31.88'	082°00.24'	
Caesar['s] Creek Bank	25°23.035'	080°12.629'	day beacon TR 10 in middle of channel through Caesar Creek Bank
Cape Florida (Lighthouse)	25°39.999'	080°09.366'	[abandoned]
Cape Sable (East Cape Light)	25°04.996'	081°04.949'	flashing red buoy no. 2
Carysfort Reef (Lighthouse)	25°13.324'	080°12.685'	
Conch Reef	24°56.984'	080°27.497'	red nun buoy no. 12
Drago Key [see Rodríguez Key]			
Dry Tortugas (Garden Key) Lighthouse at Ft. Jefferson	24°37.689'	082°52.338'	[abandoned]
Dry Tortugas (Loggerhead Key) Lighthouse	24°37.911'	082°55.315'	
Elliot Key (Caesar['s] Creek)	25°23.662'	080°13.840'	Elliot Key Light TR 20 at entrance to Caesar Creek
Fowey Rocks Lighthouse	25°35.443'	080°05.807'	
Hillsboro Inlet Lighthouse	26°15.548'	080°04.836'	
Indian Key (center of)	24°52.69'	080°40.62'	
Key Vaca	24°43.55'	081°03.06'	taken at Marathon Airstrip
Key West (East Martello Tower)	24°13.14'	081°45.29'	
Key West Lighthouse	24°33.036'	081°48.057'	[abandoned]
Key West Main Ship Channel (entrance)	24°27.685'	081°47.990'	red whistle buoy "KW"
Key West Northwest Channel (entrance)	24°38.867'	081°53.956'	flashing green buoy no. 1
Key West Southwest Channel	24°28.529'	081°54.780'	red nun buoy no. 2
Knight['s] Key (west end of)	24°42.421'	081°07.48'	
Long Key	24°29.27'	080°49.10'	radio tower
Looe Key (also as "Loue Key") Light	24°32.809'	081°24.158'	
Lower Matecumbe Key	24°54.30'	080°38.88'	radio tower
Miami (Bear Cut)	25°43.575'	080°08.030'	red day beacon no. 2
Miami (Government Cut)	25°45.580'	080°07.273'	red main channel buoy No. 8
Middle Sambo Reef	24°29.40'	081°40.51'	
Old Rhodes Key (center of east shore)	25°22.10'	080°14.14'	
Pickles Reef	24°59.29'	080°24.98'	
Ragged Keys	25°31.90'	080°10.25'	
Rodriguez Key (northeast anchorage)	25°03.31'	080°26.99'	
Sand Key Lighthouse	24°27.274'	081°52.475'	
Sombrero Key Lighthouse	24°37.675'	081°06.641'	
Stock Island	24°34.30'	081°44.41'	radio tower
Tavernier Key (northside anchorage)	25°00.09'	080°29.85'	
Triumph Reef Light	25°28.639'	080°06.734'	
Turtle Harbor	25°16.339'	080°13.691'	red day beacon no. 6
Upper Matecumbe Key	24°54.30'	080°38.88'	radio tower
Western Dry Rocks Reef	24°26.76'	081°55.61'	

boat, the *Eolis*, made a single dredge haul off Key West, Florida, in 90 fathoms"). Early batches given to USNM were alphabetically organized while most material was entered into a numerical system. Certain blocks of numbers were reserved for special projects or localities (for instance, the 200 series of numbers was apparently used for Cuban material, regardless of chronological sequence).

An initial goal of our project was to give full geodetic data for all of the *Eolis* stations to facilitate GIS-based information retrieval systems. However, as outlined above, the locality data as currently reconstructed have greatly different levels of accuracy and interpretability and we have instead opted for a textual description of the individual circumstances for each station. Many collecting events described in the logs have various problems and uncertainties attached. Certain station descriptions in the log are quite specific (e. g., "west of Sand Key until 95 fms by sounding, Sand Key bearing NE by N $^1/_2$ N"; *Eolis* log entry, 31 May 1916). Henderson's descriptions use compass bearings from major landmarks in the directional point system in common use before World War II. This point system employs the well-known cardinal points of the compass card (N, E, S, W; with N corresponding to 0º00' and 360º00'), as well as intercardinal points (e. g., NE at 45º00'), combination points (e. g., NNE at 22º30'), and by-points (e. g., NE by N at 33º45'). We have included all such information in the station descriptions in Table 1. In addition, to facilitate location of the *Eolis* stations, coordinates are provided for major landmarks (e. g., lighthouses, other tall land-based structures, major channel buoys, reefs, etc.; Table 2).

Other logged data are decidedly less precise: "ran out a mile or two to presumably 80-90 fms and made a haul" (*Eolis* log entry, 21 April 1910). Theoretically, some of these uncertainties could be individually narrowed, by presuming prevailing winds and currents on that particular day in that particular region, by reconstructing additional potential locations of landmarks mentioned by Henderson, by assuming depth contours for the sandy and muddy areas that are not covered by contemporary charts, and by guessing whether Henderson on that particular day based his log entries on sounded or charted depths (but such an exercise would only make sense under exceptional circumstances, such as the need to recollect a type locality).

Table 1 summarizes the results of our attempt to match dated *Eolis* log entries, Henderson's sample bag numbers, and the Smithsonian station list. Our list was augmented by specimen label data (containing information that went beyond the log book entries and the Smithsonian list, and may have been provided by Henderson when the material came to the Smithsonian). We expect that additional such information will surface over time, with subsequent workers studying the vast numbers of *Eolis* specimens in the Smithsonian collection - a task that we could not practically accomplish within the current project.

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Shell damage in salt marsh periwinkles (*Littoraria irrorata* [Say, 1822]) and resistance to future attacks by blue crabs (*Callinectes sapidus* [Rathbun, 1896])

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Abstract: Unsuccessful predation by the blue crab (*Callinectes sapidus* [Rathbun, 1896]) on salt marsh periwinkle snails (*Littoraria irrorata* [Say, 1822]) could result in shell damage and the subsequent development of a visible shell scar. We experimentally determined whether scarred *L. irrorata* are more or less resistant to blue crab predation than unscarred individuals. We simultaneously presented equal numbers of similar-sized scarred and unscarred snails to individual blue crabs and recorded the number of each type of snail consumed. We also compared shell attributes of scarred and unscarred snails from two marsh sites on Sapelo Island, Georga, U. S. A. Crabs consumed significantly more unscarred than scarred snails, suggesting that unscarred snails are more easily accessed. This pattern was more pronounced when the snails were close to the maximum edible size. Measurements indicated that the shells of scarred snails had significantly thicker lips than those of unscarred snails. These results demonstrate that shell scars correlate with greater predation resistance in *L. irrorata*.

Key Words: predation, *Littoraria, Callinectes*, shell repair, salt marsh

Animals have evolved a variety of defensive morphological traits that confound the capture and handling efforts of their predators. Morphological adaptations can derive from natural selection for a particular structure or trait, or from plastic morphological responses to encounters with risk (Vermeij *et al.*, 1981; Dodson, 1989). Although not extensive, most research on plastic morphological responses focuses on how organisms adapt after sensing chemical cues that signal the presence of a predator (Appleton and Palmer, 1988; Dodson *et al.*, 1994; Lewis and Magnuson, 1999; Trussell and Smith, 2000). In this paper, we examine another mechanism by which the morphology of prey might respond to predation risk. We investigate whether prey morphology is distinct between prey that have had injurious, nonlethal encounters with a predator versus prey that have not been previously injured. In the case of repair following an injury, the defensive capacity of any damaged structures may be compromised or improved.

Snails display a wide range of behavioral and morphological antipredatory adaptations (Appleton and Palmer, 1988; Covich *et al.*, 1994; Lewis and Magnuson, 1999; Turner *et al.*, 1999). Morphological adaptations that increase handling time may ultimately reduce predation risk. In environments with high predation risk, natural selection has resulted in some snail species developing thick shells, narrow apertures, and reduced spires. These traits increase handling difficulty for crushing predators such as crabs (Vermeij and Covich, 1978; Palmer, 1979; Bertness and Cunningham, 1981). At time scales much shorter than that of natural selection, individual snails may develop stronger shells in response to chemical cues released by the feeding activities of decapods (Appleton and Palmer, 1988; Trussell and Smith, 2000), although this process is not universal (Lewis and Magnuson, 1999).

For marsh periwinkles (*Littoraria irrorata* [Say, 1822]), behavioral adaptations reduce predator encounter rates (Hamilton, 1976; Warren, 1985; Dix and Hamilton, 1993). Morphological antipredatory adaptations, however, have not been demonstrated for *L. irrorata*. For example, Blundon and Vermeij (1983) compared the shell strength of *L. irrorata* that had survived previous attempts at predation by blue crabs (*Callinectes sapidus* [Rathbun, 1896]), as indicated by scars on the shell (Vermeij, 1978), with snails lacking any indication of ever encountering a predator. Pressing the ultimate body whorl with an Instron testing device, they found no difference in shell strength between the two classes of snail. Crabs employ many forms of attack when foraging on snails (Hamilton, 1976; Bertness and Cunningham, 1981; Vermeij, 1982a). For example, *C. sapidus* prey on relatively large snails by progressively chipping away at the aperture lip, rather than applying force to the ultimate body whorl (Schindler *et al.*, 1994). We investigate here whether the presence of a scar correlates with snail vulnerability to crab predation.

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Predation pressure by crabs on snails and injury rates of snails are greater at lower elevation sites within a given marsh (Schindler *et al.*, 1994), and this difference may have consequences for shell morphometry. Larger crabs, which have higher predation success rates for a given sized snail, may occur at lower elevation marshes (Schindler *et al.*, 1994). To evaluate the general effect of scarring on morphometry across disparate sites, we examined the effect of scar presence on morphometry at both a low and a high elevation site. To evaluate the effect of scarring on predation success across a range of predator strengths, we examined predator success across a wide range of crab and snail sizes.

Blue crabs display size preferences and will discard snails that are too large to handle (Hamilton, 1976; Schindler *et al.*, 1994). As the crab carapace width / snail shell length ratio (crab / snail size ratio) increases above 6.4, most snails are crushed and consumed by crabs. Below this ratio (i.e., when a snail is relatively large for a given crab) there is a linear decrease in the likelihood of a shell being crushed (Schindler *et al.*, 1994). We predict that if the presence of a scar influences the vulnerability of snails to predation, this effect would be manifest below crab / snail size ratios of 6.4. Below this ratio, subtle differences in morphology will have discernable effects on vulnerability to successful attack. Above this ratio all snails would be extremely vulnerable, independent of scarring status.

We conducted laboratory tests and morphometric measurements to determine whether the presence of a scar in the shells of *Littoraria irrorata* correlates with differential predation success by *Callinectes sapidus*. To test the null hypothesis that scarring does not correlate with crab predation success, we investigated whether blue crabs consumed significantly more scarred or unscarred snails of similar size. To determine if relative consumption rate was related to crab size, snail size, or crab/snail size ratio, we investigated whether differences were more apparent for specific subsets of the experimental populations. Finally, we measured aperture and lip characteristics of scarred and unscarred *L. irrorata* to identify differences in shell traits between scarred and unscarred snails.

METHODS

Consumption comparison

We conducted an experiment to test whether blue crabs more readily consumed scarred or unscarred snails. We collected all experimental *Littoraria irrorata* from a 180 m^2 region of Dean Creek Marsh, Sapelo Island, Georgia, USA. We measured snail shell length to the nearest millimeter with calipers, and examined snails for the presence of a scar (a jagged line associated with a visible indentation in the shell). The snails used in feeding experiments ranged in size from 14 to 22 mm. We collected crabs from South End Creek Marsh and from the coastal beach southeast of Dean Creek. We transferred crabs to a large flow-through holding tank and conditioned them to the laboratory environment for at least 48 hr, during which time they were not fed. After the acclimation period, individual crabs were transferred to separate flow-through glass aquaria.

We conducted 33 feeding experiments using 13 crabs (1 to 6 experiments per crab; Table 1). In each experiment, we simultaneously presented an individual crab with 10 snails of equal length, 5 that had shell scars and 5 that did not. We continued an individual feeding experiment until the crab had consumed at least 3 snails or had ceased feeding for at least 15 min. After completion of an experiment, we recorded the number of remaining scarred and unscarred snails. A number of experiments using separate crabs in separate aquaria were conducted simultaneously. We did not reuse snails for any experiment and we removed from our analysis experiments in which crabs did not consume any snails.

To determine whether scarring status influenced the number of snails consumed, we ran a G-test on the pooled data from the 33 experiments (Sokal and Rohlf, 1995). Because crabs were presented with 10 snails in each experi-

Table 1. Blue crab carapace width (mm), snail shell length (mm), and total number of snails presented to each crab. In each experiment, five scarred and five unscarred snails were presented. When more than one experiment was performed at a given size, the number of experiments is listed in parentheses.

Carapace Width (mm)	Snail Sizes (mm) (Number of Experiments)	Total Number of Snails Presented
82.2	16	10
86.7	14, 15, 16(2)	40
102.2	14(2), 16(2), 17(2)	60
106.8	17, 18	20
113.5	17, 18(2)	30
118.3	19, 20	20
119.2	17(2), 18(2)	40
121	18, 21	20
124.2	17, 18	20
129.7	19	10
132.4	20, 21	20
133	15, 20	20
134.6	20, 22	20

ment, for the G-test we define each individual snail as an observation, generating a total sample size of 330 observations. We compared the total number of scarred and unscarred snails eaten with the null hypothesis that equal numbers of each would be consumed. We used heterogeneity G-tests to evaluate whether consumption of snails by individual crabs deviated significantly from the experimental crab population, or whether the consumption of snails by individual crabs varied among experiments (Sokal and Rohlf, 1995).

We recognized that scarring status might not affect crab predation success for very small, easily crushed snails. Thus, we intentionally conducted multiple experiments above and below a critical crab / snail size ratio (6.4), determined experimentally by Schindler *et al.* (1994). We also intentionally used a broad range of crab and snail sizes in order to separately examine the effect of crab and snail size. In total, we conducted 15 experiments above and 18 experiments below the critical size ratio. We also examined the results for statistical significance when data were separately pooled by median snail or crab size. The median sizes (18 mm for snails and 115 mm for crabs) are sizes at which predation success by *Callinectes sapidus* on *L. irrorata* changes significantly (e.g., see table 3 in West and Williams [1986] and fig. 9 in Schindler *et al.* [1994]).

Shell morphometry

We compared shell characteristics of 257 unscarred and 48 scarred snails collected from a site with high predation risk and a site with low predation risk. All snails were collected in late October, 1999. The site with high predation risk, Lighthouse Marsh, is located along the shore of Doboy Sound, a source of crabs for these intertidal marshes. By contrast, predation risk is reduced at North End Marsh, a higher elevation site located at the headwaters of Dean Creek about 3 km from Doboy Sound (Schindler *et al.*, 1994). We captured and measured 113 unscarred snails and 27 scarred snails from Lighthouse Marsh and 144 unscarred and 21 scarred snails from North End Marsh. We measured shell traits to the nearest 0.01 mm using a dial caliper. The attributes measured were shell length, aperture length, aperture width, and lip thickness (see axis orientations in figure 1 of Janson and Sundberg [1983]). Aperture length and width were the distances between the inner surfaces of the aperture along these axes. For lip thickness, measurements were collected at least three times on separate randomly selected locations 1 mm inside the lip edge and the minimum value was recorded. Particular traits were occasionally, and inadvertently, not measured for a few snails, resulting in a sample size of between 297 and 305 measured snails per trait. In addition, we estimated the shape of the aperture as an ellipse, and calculated aperture area from the measurements of aperture length and width.

We used general linear models to determine the relative importance of collection site and scarring status on aperture length, aperture width, aperture area, and lip thickness (Draper and Smith, 1998). These morphological traits scale with overall shell length (see Results section). Therefore, we first de-trended the data for the effect of length by fitting a linear regression of each trait vs. shell length and then taking the residuals. For each trait, these residuals were checked for normality and then analyzed as a function of site, scarring status, and the site x scarring status interaction.

RESULTS

Consumption comparison

In all experiments combined, 165 scarred and 165 unscarred snails were presented to the blue crabs. Of these, the crabs ate 76 scarred and 98 unscarred snails, a significant difference ($p < 0.025$; Table 2). When the crab or snail population was examined by size, crabs ate more unscarred than scarred snails, but the pattern was only significant for small (< 18 mm) snails (Table 2). No heterogeneity was observed between individual crabs and the entire experimental population. Furthermore, no heterogeneity was found between trials, indicating that crab behavior was consistent among trials.

Crabs consumed fewer scarred snails in trials when the crab to snail size ratio was small (Fig. 1). Individual G tests indicated significance for the low size ratio but not for the high size ratio crabs (Table 2). In trials characterized by high body size ratios (i.e. relatively small snails), predation rates were uniformly high at around 60%, with only an 8% decrease for scarred snails.

Shell morphometry

Aperture length, aperture width, aperture area, and

Table 2. Consumption percent differences (percent of unscarred snails consumed minus the percent of scarred snails consumed) and G-test results for all trials and for subsets of the sample categorized according to snail shell length (large ≥ 18 mm > small), crab carapace width (large ≥ 115mm > small), and crab / snail size ratio.

Sample Type (N)	Consumption Percent Difference (Unscarred - Scarred)	G
All Trials (330)	13	5.90*
Large Snails (160)	10	1.60
Small Snails (170)	18	5.37*
Large Crabs (170)	13	2.87
Small Crabs (160)	15	3.62
Crab / Snail Size Ratio < 6.4 (180)	19	6.46*
Crab / Snail Size Ratio > 6.4 (150)	8	0.98

* indicates significance at $\alpha = 0.025$

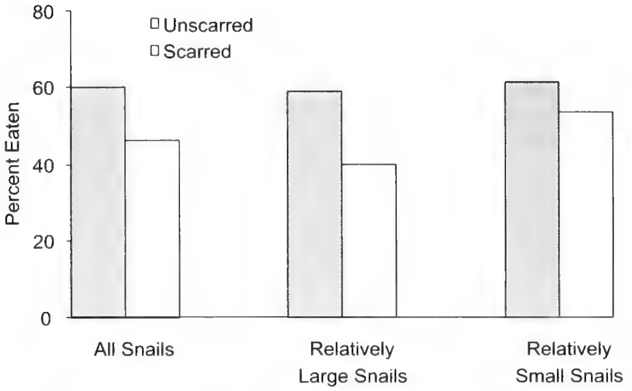

Fig. 1. The percentage of all snails eaten (N = 330), and the percentage of relatively large (N = 180) and relatively small (N = 150) snails eaten. The relatively large snails have a crab / snail size ratio below 6.4 and the relatively small snails have a crab / snail size ratio above 6.4.

lip thickness all scaled positively with shell length (R^2 = 0.87, 0.79, 0.85, and 0.67, respectively; linear regression $p < 0.001$ in all cases). Probability plots indicated that all four sets of residuals followed a normal distribution. After removing the effect of shell length, we determined the interactive effect of site (high vs. low predation risk) and scarring status on each of these three shell traits. Aperture length was reduced in snails collected from Lighthouse Marsh ($p < 0.001$), the site with high predation risk, and was reduced in snails bearing a scar ($p = 0.039$; Fig. 2A). The interactive effect of site and scarring status was not significant at $p = 0.05$.

There was an interactive effect of site and scarring status on aperture width ($p = 0.017$). On scarred snails, aperture width was increased at Lighthouse Marsh, where predation risk was allegedly higher. By contrast, the aperture width of scarred snails was reduced at the site with low predation risk, North End Marsh (Fig. 2B).

Variability in aperture area was not explained by site, scarring status, or their interaction ($p > 0.05$; Fig. 2C).

Finally, lip thickness was greater at the site with high predation risk ($p = 0.016$), and was greater on snails bearing a scar ($p = 0.023$; Fig. 2D). There was no interactive effect on lip thickness.

DISCUSSION

The blue crabs used in this experiment ate significantly more unscarred than scarred snails. Additionally, scarred snails had thicker lips and differently shaped apertures than unscarred snails. Integration of these results suggests two hypotheses: first, following an attack, repair results in a shell with an improved defensive capacity; second, lip thickness is inversely related to vulnerability. In the following discussion, we further evaluate these hypotheses.

Our data suggest that snails that have experienced predation attempts have shells with an improved capacity for defense. This improvement probably lies in the increase in lip thickness, but does not derive from any changes in aperture shape. Apertures were shorter on scarred snails. In some cases, however, apertures were also wider. These changes in aperture shape result in no net change in aperture area. Consequently, scarring status likely has little effect on a crab's ability to insert its chelae into the aperture in attempts to chip the shell. Chelae insertion is more frequently used by crabs to access large snails (Schindler *et al.*, 1994). Therefore, the more significant difference in predation success between scarred and unscarred snails below 18 mm than above 18 mm supports the hypothesis that chelae insertion success does not depend on scarring status.

Increase in the thickness of the aperture lip, however, would influence a crab's ability to chip a snail shell. Our data provide evidence for the hypothesis that thicker lips endow snails with greater resistance to predation. In the field, snails with scars had thicker lips, and in our experiment, snails with scars were eaten less frequently. Furthermore, Blundon and Vermeij (1983) demonstrate that overall strength of the shell's body whorl does not significantly differ between scarred and unscarred snails, implicating a more isolated morphological mechanism, such as differences in lip thickness.

The increased lip thickness of scarred snails could result from at least two mechanisms. First, scarred snails may have inherited greater resistance, regardless of scarring status, as evidenced by their survival of a previous predation attempt. In other words, the scarred population represents the skewed result of natural selection due to removal of weak shelled individuals from the entire population (Vermeij, 1982b; Johannesson and Johannesson, 1996). Second, morphological responses may be induced by unsuccessful attacks. A scarring event may lead to the development of antipredatory morphology in individual snails (Appleton and Palmer, 1988). This hypothesis is supported by the work of Trussell and Smith (2000), who demonstrate shell thickening of *Littorina obtusata* in response to predator effluent across a wide geographic range. Regardless of the mechanism, because *Littoraria irrorata* exhibit a planktonic larval stage (Bingham, 1972), spatial variation in lip thickness would only be maintained by adult exposure to predation gradients after settlement.

Our data also suggest that snail shell attributes are influenced by predation risk regardless of whether an individual snail is attacked. Snails collected from Lighthouse Marsh, where predation risk is high, had shorter apertures and thicker lips than snails collected from the less risky North End Marsh site. Both scarred and unscarred snails demonstrated this pattern. Snails may have differed

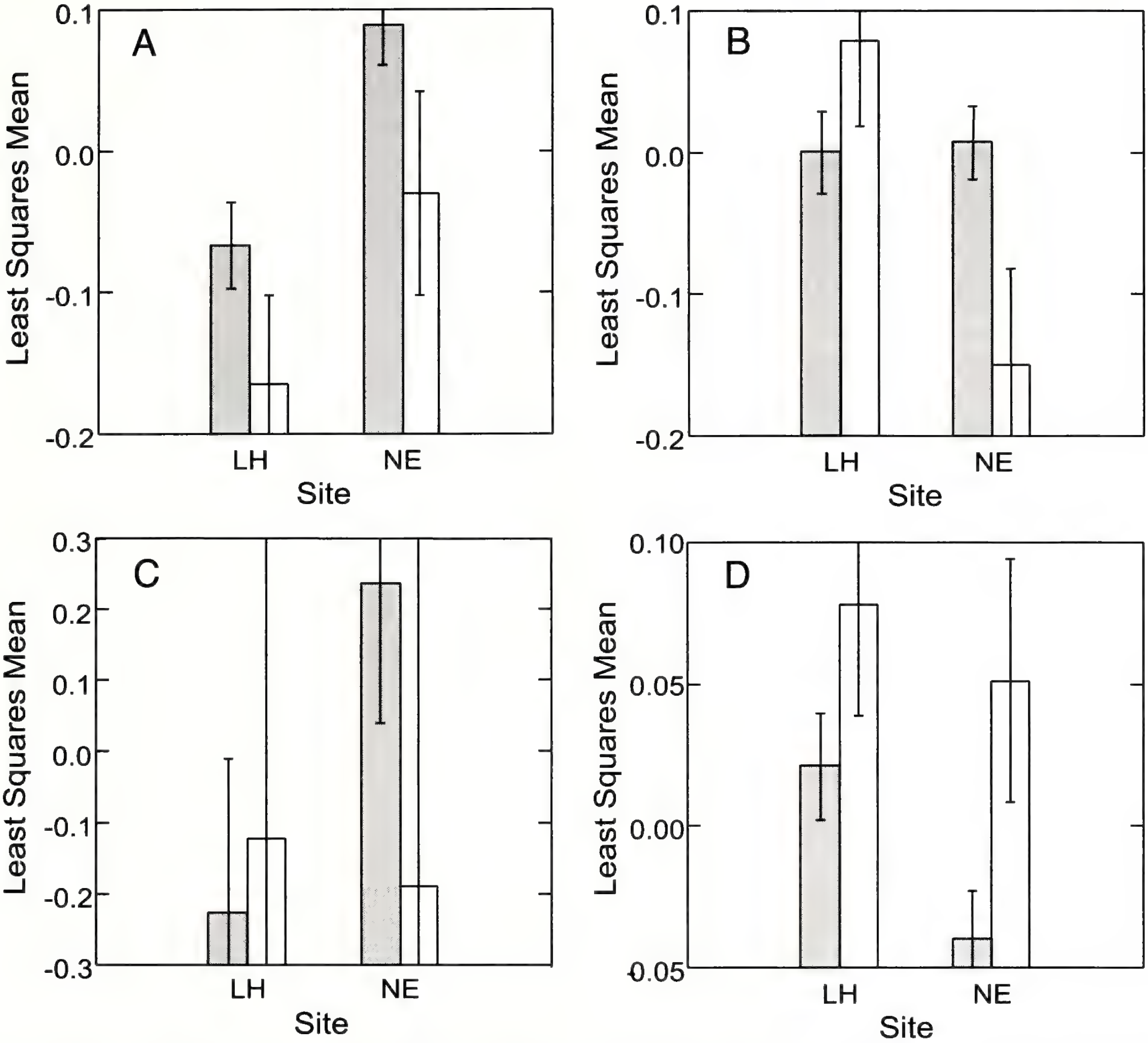

Fig. 2. Relationships of traits of snail shells with site (Lighthouse Marsh, LH - high predation risk; North End Marsh, NE - low predation risk) and scarring status (open bar - scarred; dark bar - unscarred). A site with high predation risk (Lighthouse Marsh, LH) and a low predation risk site (North End Marsh, NE) were sampled for scarred and unscarred snails. Shell traits include (A) aperture length (number of snails, N = 305), (B) aperture width (N = 300), (C) aperture area (N = 300), and (D) lip thickness (N = 297). Bars indicate the least-squares means of an ANOVA of shell trait as an interactive function of site and scarring status. Error bars = 1 SE. Data are the residuals from a linear regression of shell trait vs. shell length.

between sites in these morphological traits for two reasons. First, selective pressures would be greater at Lighthouse Marsh. Second, snails may respond to chemical cues indicative of risk that are released by crabs (Trussell and Smith, 2000). We only have one site apiece characterized by high and low predation risk. Thus, we submit only as a suggestion that periwinkle morphology responds to predation risk in the absence of an actual scar-inducing encounter. Nevertheless, natural selection for improved defensive capacity is a pervasive, widespread process in gastropod-decapod systems (e.g., Kitching and Lockwood, 1974).

Differences in the vulnerability of scarred and unscarred snails were particularly evident when snails were close to the maximum edible size (i.e. when the crab / snail size ratio was less than 6.4). This is consistent with Elner and Hughes' (1978) demonstration that for crabs, the cost of handling prey changes more rapidly at high prey sizes. In the context of optimal foraging theory (Pyke *et al.*, 1977), our results suggest that the difference in overall energetic gain between scarred and unscarred snails is most pronounced at the maximum edible snail size. At this size ratio, the subtle morphometric differences associated with scarring have the greatest effect.

There are several possible consequences of shell damage for *Littoraria irrorata*. First, as noted above, scarred snails have thicker lips than unscarred snails. This increased lip thickness may be a barrier to efficient consumption by blue crabs. Second, snails may suffer a trade-off between repairing the shell and various physiological processes. For instance, the energetic cost of repair may compromise reproductive output and growth. Stahl and Lodge (1990), however, found no such trade-off in one freshwater species, and inferred that population growth was not compromised by nonlethal injuries. Third, it is possible that increases in lip thickness associated with scarring may reduce soft tissue mass, causing a reduction in the energetic value of snails for crabs.

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Reproductive biology of four freshwater mussels (Bivalvia: Unionidae) endemic to eastern Gulf Coastal Plain drainages of Alabama, Florida, and Georgia

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Abstract: The reproductive biology and glochidial shell morphology of three federally endangered freshwater mussels, the fat threeridge, *Amblema neislerii*; Gulf moccasinshell, *Medionidus penicillatus*; and oval pigtoe, *Pleurobema pyriforme*; and one federally threatened mussel, the purple bankclimber, *Elliptoideus sloatianus*, were studied from May 1995 to June 1997 in the Apalachicola, Flint, and Ochlockonee river drainages of Florida and Georgia. Gravid *A. neislerii* were found in early June. Laboratory experiments indicated that five fish species served as hosts: weed shiner, *Notropis texanus*; bluegill, *Lepomis macrochirus*; redear sunfish, *L. microlophus*; largemouth bass, *Micropterus salmoides*; and blackbanded darter, *Percina nigrofasciata*. *Elliptoideus sloatianus* were found gravid from late February through mid-April. None of the 14 fish species exposed to *E. sloatianus* glochidia resulted in the identification of a primary host fish. *Medionidus penicillatus* were found gravid during September, November, March, and April. The brown darter, *Etheostoma edwini*, and blackbanded darter, *Percina nigrofasciata*, were identified as primary host fishes for *M. penicillatus*. *Pleurobema pyriforme* were found gravid from March through July. Only the sailfin shiner, *Pteronotropis hypselopterus*, was identified as a primary host fish for *P. pyriforme*. Glochidial shell morphology of *A. neislerii, M. penicillatus*, and *P. pyriforme* were similar to other species in their respective genera. The glochidia of the monotypic species *E. sloatianus* were morphologically most similar to *Epioblasma brevidens* and *E. capsaeformis*.

Key Words: Unionidae, freshwater mussel, host fish, reproductive biology, glochidia, shell morphology, endangered and threatened species

Historically, North America was known for its rich mussel fauna, with about 300 species recognized (Turgeon *et al.*, 1998). Since the early 1900s, at least 7% of the mussel fauna has become extinct, more than 40% are federally listed as endangered or threatened, 24% are of special concern, and the status of 5% is undetermined (Williams and Neves, 1995). The reasons for this decline are not well understood. The primary cause is thought to be loss of suitable habitat, caused by increased siltation and dredging, introductions of nonindigenous species, and pollution (Ortmann, 1909; Fuller, 1974; Williams *et al.*, 1993). In addition, most freshwater mussels are obligate parasites on fish, and recent declines in the North American fish fauna may also have negative effects on mussel populations (Allan and Flecker, 1993).

Knowledge of the reproductive biology of many freshwater mussels remains incomplete (Jansen, 1990). For example, host fish for only 25% of the 300 mussel species in North America have been identified (Watters, 1994), although recent studies are gradually expanding that number (Weiss and Layzer, 1995; Haag and Warren, 1997; Keller and Ruessler, 1997; Roe and Hartfield, 1997). Host fish information is lacking for most of the southeastern mussel fauna, an area where roughly 90% of the freshwater mussel species occur (Neves *et al.*, 1997).

Understanding the reproductive biology, especially host fish, is an important part of any freshwater mussel recovery or management plan. However, many fish are reported as hosts regardless of the number of juvenile mussels that they successfully metamorphose. This information may be misleading, for example, a fish species metamorphosing an average of 0.1 juvenile mussels per fish compared to another fish species metamorphosing an average of 100 juvenile mussels per fish are both reported as a "host fish." Considering the difference in the average number of metamorphosed juveniles between these two species, it would be difficult to consider them as equally effective host fish. In an earlier host fish experiment, Hagg and Warren (1997) made an attempt to distinguish between fish that successfully metamorphosed high versus low numbers of juvenile mussels as "host fish" as opposed to "marginal host fish." In looking at host fish suitability for *Ligumia recta*, Khym and Layzer (2000) also noted varying levels of successful transformation for different species of fishes.

However, these and other host fish studies offer no quantitative limits, such as average number of juvenile mussels per host fish, for the various categories that are identified based on successful transformation rates. The criteria to define primary and secondary host fish proposed by O'Brien and Brim Box (1999) were utilized in this experiment.

In 1998 the fat threeridge, *Amblema neislerii* (I. Lea, 1858); Gulf moccasinshell, *Medionidus penicillatus* (I. Lea, 1857); and oval pigtoe, *Pleurobema pyriforme* (I. Lea, 1857), were listed as federally endangered and the purple bankclimber, *Elliptoideus sloatianus* (I. Lea, 1840), was listed as federally threatened as a result of a dramatic decline in their historic ranges (USFWS, 1998). These species are endemic to eastern Gulf Coastal Plain drainages of Alabama, Florida, and Georgia (Clench and Turner, 1956; Butler, 1989; Williams and Butler, 1994). Knowledge of the reproductive biology of these freshwater mussels is needed to aid resource managers in the conservation and recovery activities. The objectives of this study were to: determine the period when glochidia are present in the gills; identify the host fish via laboratory experiments; and, using scanning electron microscope (SEM) photographs, qualitatively describe glochidial shell morphology to determine if there are unique glochidial characters useful for species identification.

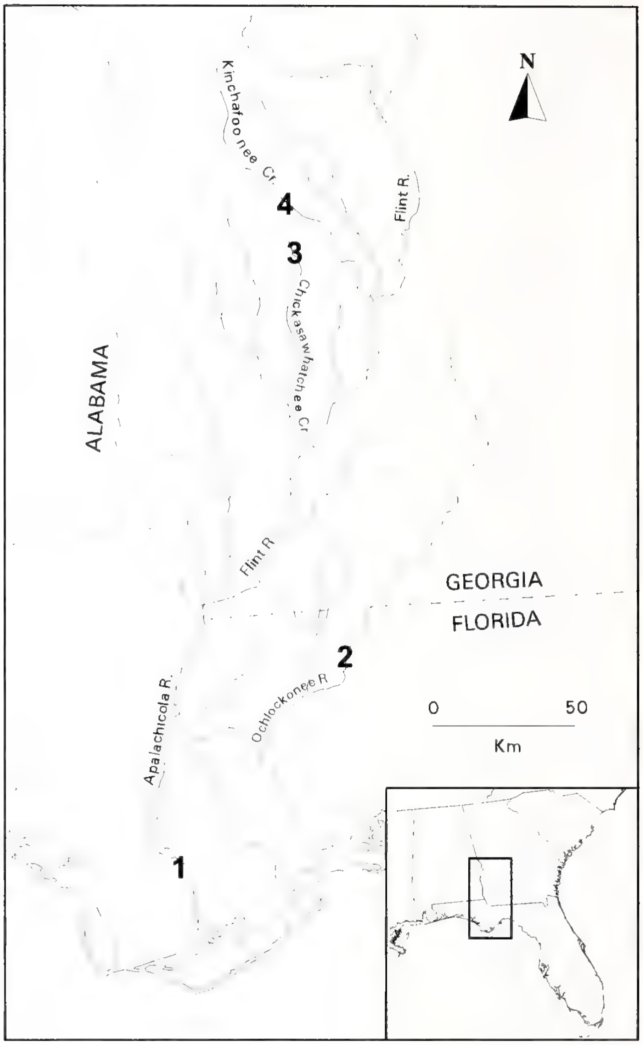

Fig. 1. Collection localities for mussel specimens used to harvest glochidia. *Amblema neislerii* were collected from site 1 (Apalachicola River); *Elliptoideus sloatianus* were collected from site 2 (Ochlockonee River); and *Medionidus penicillatus* and *Pleurobema pyriforme* were collected from sites 3 and 4 (Chickasawhatchee and Kinchafoonee Creeks).

MATERIAL AND METHODS

The study sites were located in the Apalachicola River, Franklin County, Florida; the Ochlockonee River, Leon County, Florida; and two tributaries of the Flint River: Chickasawhatchee Creek, Terrell County, Georgia; and Kinchafoonee Creek, Webster County, Georgia (Fig. 1). These streams are all located in the Coastal Plain Physiographic Province. Like most Coastal Plain streams, they have low to moderate gradient with sand or sand mixed with gravel substrate, hardwood floodplains, and short hydroperiods (Hubbard *et al.*, 1990).

Amblema neislerii were collected from the Apalachicola River and *Elliptoideus sloatianus* were collected from the Ochlockonee River. *Medionidus penicillatus* and *Pleurobema pyriforme* were collected from Chickasawhatchee and Kinchafoonee creeks. The streams were visited monthly and individual mussels (10-20) were inspected for the presence of glochidia from May 1995 to June 1997. When a target mussel was found it was gently opened by hand to a point that the gills could be inspected to determine if they were swollen, indicating the presence of glochidia. Gravid *M. penicillatus* were easily identified by the presence of swollen gills. However, for *A. neislerii, E. sloatianus*, and *P. pyriforme*, it was difficult to determine if they were gravid by inspection in the field. To avoid misidentifying gravid individuals, 8 to 12 specimens were collected each month, separated by species, placed into zip-lock bags with creek water, and held in a cooler during their transport to the Florida Caribbean Science Center, Gainesville, Florida. In the laboratory the mussels were separated by species and held in separate 4.4 l containers with aerated well water until their glochidia were released and collected. Gravid individuals usually released their glochidia within a few weeks after they were collected.

Host fish for the four mussels were determined by laboratory experiments. Since fish can develop a natural immunity to glochidia as a result of previous infections (Reuling, 1919 as cited in Coker *et al.*, 1921), all fish used in the experiments were either purchased from fish hatcheries or collected from streams that had few or no freshwater mussels (Zale and Neves, 1982; Yeager and Neves, 1986). As an added precaution, all field-collected fish were held two weeks to allow any previously attached glochidia to transform and drop off. A total of 19 fish species representing 6 different families were collected for the study (Table 1). However, the numbers of fish and species used for the host fish experiments varied for each mussel species.

Three criteria were used to determine whether a fish species was a primary host or a secondary host for each mussel. A fish was considered to be a primary host when (1) the percentage of test fish successfully metamorphosed juvenile mussels ranged from 30-100% (0-29% for secondary hosts), (2) the average number of juveniles metamorphosed per successful fish species was equal to or greater than three, and (3) the fish species occurred in the same stream as the mussel and would likely encounter the mussel's glochidia (O'Brien and Brim Box, 1999). Fish species successfully metamorphosing glochidia, but failing to meet any of these criteria were identified as secondary host fish. Due to space limitations, the fish were not held separately (one fish per container) during the host fish experiments for *Amblema neislerii* and primary host fish were not determined for this mussel. A fish metamorphosing juvenile *A. neislerii*, without regard to the number of juveniles metamorphosed, was considered to be a host fish. If a fish metamorphosed juvenile mussels, but did not occur in the same stream as *A. neislerii*, it was considered to be a secondary host.

Table 1. The scientific and common names of the fishes used in the host fish identification experiment. *Moxostoma robustum* (*) is outside the native range of mussels used in this experiment. Five species (**) were from cultured stock and had never been exposed to unionid mussels.

Scientific Name	Common Name
CYPRINIDAE	
Notropis harperi	redeye chub
Notropis petersoni	coastal shiner
Notropis texanus	weed shiner
Opsopoeodus emiliae	pugnose minnow
Pteronotropis hypselopterus	sailfin shiner
CATOSTOMIDAE	
Erimyzon sucetta	lake chubsucker
*Moxostoma robustum**	robust redhorse
ICTALURIDAE	
Ameiurus natalis	yellow bullhead
*Ictalurus punctatus***	channel catfish
Noturus leptacanthus	speckled madtom
POECILIIDAE	
Gambusia holbrooki	eastern mosquitofish
*Poecilia reticulata***	guppy
CENTRARCHIDAE	
Lepomis auritus	redbreast sunfish
Lepomis gulosus	warmouth
*Lepomis macrochirus***	bluegill
*Lepomis microlophus***	redear sunfish
*Micropterus salmoides***	largemouth bass
PERCIDAE	
Etheostoma edwini	brown darter
Percina nigrofasciata	blackbanded darter

The mussel species were proposed for federal listing during this study; therefore a limited number of females was collected and non-lethal methods were used to collect the glochidia. Glochidia were collected from several *Medionidus penicillatus* by making a small incision in their gills and flushing the glochidia out with a squirt bottle. These females were successfully held in the laboratory for 4-5 weeks after this procedure was performed without any mortalities. The other mussel species used in this experiment usually expelled their glochidia while in the holding tanks. Once the glochidia or conglutinates were released they were collected by siphoning the contents from the bottoms of the holding containers through a 105 μm mesh sieve. The contents were then rinsed into a petri dish and examined. Collected glochidia were tested for viability by observing if they responded by closing their valves when a few crystals of salt were added to the water (Zale and Neves, 1982).

One to two thousand viable glochidia collected from 2 to 5 female mussels of each species were placed into a 4 l aquarium with several fish of the same species. An aeration stone was used to suspend the glochidia throughout the water column. After the fish were exposed to the glochidia for thirty minutes, they were placed in a 4 l aquarium (44 l aquaria were used for the larger fish species), so that a single fish occupied each aquarium. Individually separating the fish allowed data to be collected on the percent of fish infected and to determine the number of juvenile mussels metamorphosed by each fish. Water from the bottom of each aquarium was siphoned through a 105 μm mesh sieve every third day starting 3 days after the fish were exposed to the glochidia. The contents collected in the sieve were rinsed into a petri dish and inspected with a dissecting microscope for juvenile mussels. Metamorphosed glochidia were identified by the presence of gill buds and a ciliated foot (Karna and Millemann, 1978).

Survivorship of the glochidia, once they were released by the female, was determined by collecting several thousand viable glochidia and placing them in a 50 ml beaker with well water and an aerator. A sub-sample of several hundred glochidia was tested for viability daily. Glochidia were considered to be nonviable when most in the sub-sample failed to respond by closing their valves when salt crystals were added. The number of days viable glochidia were observed was recorded.

A sample of fully developed glochidia was collected from each mussel species, preserved in 70% ethanol, and later used for SEM photography. Tissue inside the glochidial shells was removed by soaking them in a 5% sodium hypochlorite solution for 10 minutes. The glochidial shells were then rinsed several times with tap water and preserved in 70% ethanol (Kennedy *et al.*, 1991). Preserved glochidial shells were placed on pegs with double-sided sticky carbon tape, air dried, and coated with gold. The valve (magnification ranged from 200 to 450X) and flange, a flattened area along the ventral margin of the glochidial shell (magnification ranged from 3,000 to 4,000X) with micropoints, small tooth-like projections located along the flange, were photographed for each species. Using a stereomicroscope with an ocular micrometer (20X magnification), measurements of 20 glochidial shells were made by averaging the height (dorsal to ventral), width (anterior to posterior), and dorsal margin length. Length of the glochidium was measured and recorded from the longest point of measurement.

Common and scientific names for freshwater mussels were taken from Turgeon *et al.* (1998). The common and scientific names for fishes were taken from Robins *et al.* (1991), except the genus name *Pteronotropis* was used instead of *Notropis* for the sailfin shiner and the common name robust redhorse instead of smallfin redhorse for *Moxostoma robustum* (Cope, 1870). These exceptions follow changes documented in the recent ichthyological literature.

Table 2. Host and non-host fishes for *Amblema neislerii*.

Fish species	N	Number of juveniles recovered	Mean number of juveniles per fish	Days to transformation
Notropis texanus	6	18	3	10-14
Noturus leptacanthus	3	0	0	—
Gambusia holbrooki	12	0	0	—
Lepomis macrochirus	10	267	27	10-14
Lepomis microlophus	9	131	15	10-14
Micropterus salmoides	5 (+2)	19	6	10-14
Percina nigrofasciata	6	134	22	10-14

+ Indicates the number of fish, with no encysted glochidia, that died before transformation date. The average water temperature during the experiment was 23°C ± 1.5°C.

RESULTS

Reproductive biology

Mature glochidia from *Amblema neislerii* were collected in early June 1997 (water temperature 24°C). *Amblema neislerii* glochidia were released in the laboratory in a white web-like mass. A closer inspection of the web-like mass revealed glochidia producing adhesive larval threads. When the mass of glochidia was introduced to water currents, the mass expanded and wrapped around the body of the fish, allowing the glochidia to attach to the fins. The fish were not examined to determine if gills were also infected. Glochidia remained viable for two days after being released from the mussel.

Five potential host fishes were identified from seven fish species that were exposed to *Amblema neislerii* glochidia: *Notropis texanus* (Girard, 1856), *Lepomis macrochirus* Rafinesque, 1819, *L. microlophus* (Günther, 1859), *Micropterus salmoides* (Lacepède, 1802), and *Percina nigrofasciata* (Agassiz, 1854) (Table 2). Glochidia transformation required 10 to 14 days in an average water temperature of 23°C ± 1.5°C. All of the fishes that metamorphosed juvenile mussels were considered hosts because they occurred in the same streams as *A. neislerii. Notropis texanus* metamorphosed the lowest average number of juveniles per fish ($\bar{x} = 3$), and *L. macrochirus* metamorphosed the highest average number of juveniles per fish ($\bar{x} = 27$).

Elliptoideus sloatianus released developing glochidia in early February (1996) as rigid white conglutinates. The flat conglutinates were 10 to 15 mm long, 1.5 mm wide (at the middle), approximately two glochidia thick, and tapered to points at each end (lanceolate shape). Most conglutinates were released as a single conglutinate, but a few were released as pairs, attached at one end, forming a V-shaped conglutinate. Mature *E. sloatianus* glochidia were collected from late February through mid-April (1996 and 1997), when water temperatures ranged from 8°C to 15°C. Unlike the premature rigid conglutinates, mature glochidia were released in loose clumps that easily separated when disturbed. The glochidia remained viable for three days once they were released by the female mussel.

Elliptoideus sloatianus glochidia metamorphosed into juvenile mussels during their parasitic attachment on 3 of 14 fish: *Gambusia holbrooki* Girard, 1859; *Poecilia reticulata* Peters, 1860; and *Percina nigrofasciata* (Table 3). Transformation of the glochidia required 14 to 17 days on *G. holbrooki*, 16 to 21 days on *P. reticulata*, and 20 days on *P. nigrofasciata* in an average water temperature of 20.5°C ± 3°C. Even though 50% of the *P. reticulata* exposed to glochidia metamorphosed juvenile mussels and the average number of juveniles metamorphosed was 7, it was considered a secondary host fish because it is

Table 3. Host and non-host fishes for *Elliptoideus sloatianus*.

Fish species	N	Number of fish that metamorphosed juvenile mussels	Mean number of juveniles metamorphosed per successful fish	Days to transformation	Host Fish Status
Notropis texanus	5	0	—	—	N
Pteronotropis hypselopterus	5	0	—	—	N
Moxostoma robustum	12	0	—	—	N
Erimyzon sucetta	5	0	—	—	N
Ictalurus punctatus	5	0	—	—	N
Ameiurus natalis	3	0	—	—	N
Gambusia holbrooki	7	7 (100%)	25	14-17	S
Poecilia reticulata	6 (+2)	2 (50%)	7	16-21	S
Lepomis auritus	3	0	—	—	N
Lepomis gulosus	8	0	—	—	N
Lepomis macrochirus	10	0	—	—	N
Lepomis microlophus	10	0	—	—	N
Micropterus salmoides	10	0	—	—	N
Percina nigrofasciata	6	1 (17%)	2	20	S

+ Indicates the number of fish, with no encysted glochidia, that died before transformation date. The average water temperature during the experiment was 20.5°C ± 3°C. Letters in the "Host Fish Status" column indicate the following: N = not a host fish; S = secondary host fish.

nonindigenous to the United States (Fuller *et al.*, 1999). *Gambusia holbrooki* were highly susceptible to *E. sloatianus* glochidia. All of the *G. holbrooki* (100%) exposed to *E. sloatianus* glochidia metamorphosed an average of 25 juveniles. *Gambusia holbrooki* also occurred in the same streams as *E. sloatianus*. However, *E. sloatianus* inhabits rivers with moderate current (Williams and Butler, 1994; Brim Box and Williams, 2000) while *G. holbrooki* is typically found in shallow water with little or no current. Because the habitats where *E. sloatianus* and *G. holbrooki* occur are not similar, it is unlikely that *G. holbrooki* can serve as a primary host for *E. sloatianus*. *Percina nigrofasciata* was also considered a secondary host because successful metamorphosis of glochidia occurred on 1 individual (17%) and the average number of juveniles metamorphosed per successful fish was less than 3.

Gravid *Medionidus penicillatus* were collected September and November 1995 and March and April 1996. Mature glochidia were found in March and April when water temperatures warmed to 11-13°C. During months when *M. penicillatus* were found with mature glochidia, they were observed completely out of the substrate, lying on their umbos with their white glochidia-filled gills pushed to the edge of the gaping shell, flapping their dark, thickened mantles. This behavior was observed in the field and laboratory.

Four potential host fish species for *Medionidus penicillatus* were identified from 8 fish species: *Gambusia holbrooki, Poecilia reticulata, Etheostoma edwini* (Hubbs & Cannon, 1935), and *Percina nigrofasciata* (Table 4). Metamorphosis occurred on *G. holbrooki* in 19 to 21 days, on *P. reticulata* in 30 to 32 days, on *E. edwini* in 30 to 37 days, and on *P. nigrofasciata* in 29 to 33 days. Water temperatures during the experiments were 21.5°C ± 1.5°C. The glochidia remained viable 2 days after they were collected from the female mussels.

Even though metamorphosis of glochidia occurred on 57% of the *Gambusia holbrooki*, with an average of 2.3 juveniles per fish, it was considered a secondary host. *Medionidus penicillatus* inhabits medium-sized creeks to large rivers with sand, gravel, and cobble substrates in slow to moderate currents (Brim Box and Williams, 2000), a habitat not frequented by *G. holbrooki*. Forty percent of the nonindigenous *Poecilia reticulata* exposed to *M. penicillatus* glochidia successfully metamorphosed glochidia, with an average number of 3 juvenile mussels per fish. However, *P. reticulata* was considered a secondary host fish because it is not native to the United States (Fuller *et al.*, 1999). During the host fish experiment encysted glochidia were visible on the fins of *Etheostoma edwini*, but not on the fins of *P. nigrofasciata. Etheostoma edwini* and *P. nigrofasciata* were identified as primary hosts because all of the fish (100%) exposed to the glochidia successfully metamorphosed juvenile mussels, each fish averaged over 4 juveniles, and these fish species occur in the study stream.

Gravid *Pleurobema pyriforme* were collected from March to July (1995 and 1996). Viable glochidia were collected from *P. pyriforme* in water temperatures ranging from 13°C to 25°C. Female *P. pyriforme* usually released conglutinates after several days in captivity. *Pleurobema pyriforme* conglutinates contained mature glochidia and eggs in various stages of development. The white to pinkish conglutinates were approximately 5 mm in length, consisting of a single layer of developing larvae. The conglutinate

Table 4. Host and non-host fishes for *Medionidus penicillatus*.

Fish species	N	Number of fish that metamorphosed juvenile mussels	Mean number of juveniles metamorphosed per successful fish	Days to transformation	Host Fish Status
Notropis texanus	7	0	0	—	N
Ameiurus natalis	6 (+3)	0	0	—	N
Gambusia holbrooki	7	4 (57%)	2.3	19-21	S
Poecilia reticulata	5	2 (40%)	3	30-32	S
Lepomis macrochirus	5	0	0	—	N
Micropterus salmoides	7 (+2)	0	0	—	N
Etheostoma edwini	7 (#2)	5 (100%)	14.6	30-37	P
Percina nigrofasciata	10	10 (100%)	5.3	29-33	P

# Indicates the number of fish, with encysted glochidia, that died before transformation. + Indicates the number of fish, with no encysted glochidia, that died before transformation date. The average water temperature during the experiment was 21.5°C ± 1.5°C. Letters in the "Host Fish Status" column indicate the following: N = not a host fish; P = primary host fish; S = secondary host fish.

Table 5. Host and non-host fishes for *Pleurobema pyriforme*.

Fish species	N	Number of fish that metamorphosed juvenile mussels	Mean number of juveniles metamorphosed per successful fish	Days to transformation	Host Fish Status
Notropis harperi	6 (+1)	0	0	—	N
Notropis petersoni	6 (+2)	0	0	—	N
Notropis texanus	6	0	0	—	N
Opsopoeodus emiliae	8 (+3)	0	0	—	N
Pteronotropis hypselopterus	11 (+2)	5 (63%)	4.2	20-25	P
Ameiurus natalis	6 (+4)	0	0	—	N
Gambusia holbrooki	6	3 (50%)	3.3	18-21	S
Poecilia reticulata	6	1 (17%)	2	19	S
Lepomis macrochirus	6	0	0	—	N
Micropterus salmoides	6 (+1)	0	0	—	N
Percina nigrofasciata	6	0	0	—	N

+ Indicates the number of fish, with no encysted glochidia, that died before transformation date. The average water temperature during the experiment was 23°C ± 3°C. Letters in the "Host Fish Status" column indicate the following: N = not a host fish; P = primary host fish; S = secondary host fish.

was not a true lanceolate shape; one end was slightly rounded. *Pleurobema pyriforme* glochidia remained viable for 3 days after being released by the female.

Three potential host fishes for *Pleurobema pyriforme* were identified from 11 species: *Pteronotropis hypselopterus* (Günther, 1868), *Gambusia holbrooki*, and *Poecilia reticulata* (Table 5). Transformation of glochidia occurred in 20 to 25 days on *P. hypselopterus*, 18 to 21 days on *G. holbrooki*, and 19 days on *P. reticulata*. The average water temperature during the transformation period was 23°C ± 3°C. Fifty percent of the *G. holbrooki* successfully metamorphosed glochidia and the average number of juveniles metamorphosed was 3.3 per fish. However, it was considered a secondary host fish because *P. pyriforme* are found in moderate current in midchannel areas of streams (Brim Box and Williams, 2000), an unlikely habitat for *G. holbrooki*. *Poecilia reticulata* was considered a secondary host because only 17% of the fish successfully metamorphosed glochidia and the average number of juvenile mussels per fish was 2. Only *P. hypselopterus* was identified as a primary host for *P. pyriforme* because 63% successfully metamorphosed glochidia and the average number of juveniles was 4.2 per fish.

Glochidial shell morphology

The glochidial valves of *Amblema neislerii* are subelliptical (Fig. 2A). The length of each glochidial valve is 204 ± 8.9 μm (180-220 μm), the height is 212 ± 5.7 μm (200-219 μm), and the straight dorsal margin is 143 ± 4.4 μm (135-149 μm). The ventral margin is curved outward (Fig. 2B). The shell surface is mostly smooth, and pitting (small holes on the surface of the shell) is minimal. Hooks are lacking. Lanceolate micropoints cover 80% of the flange. The micropoints are in irregular vertical rows that

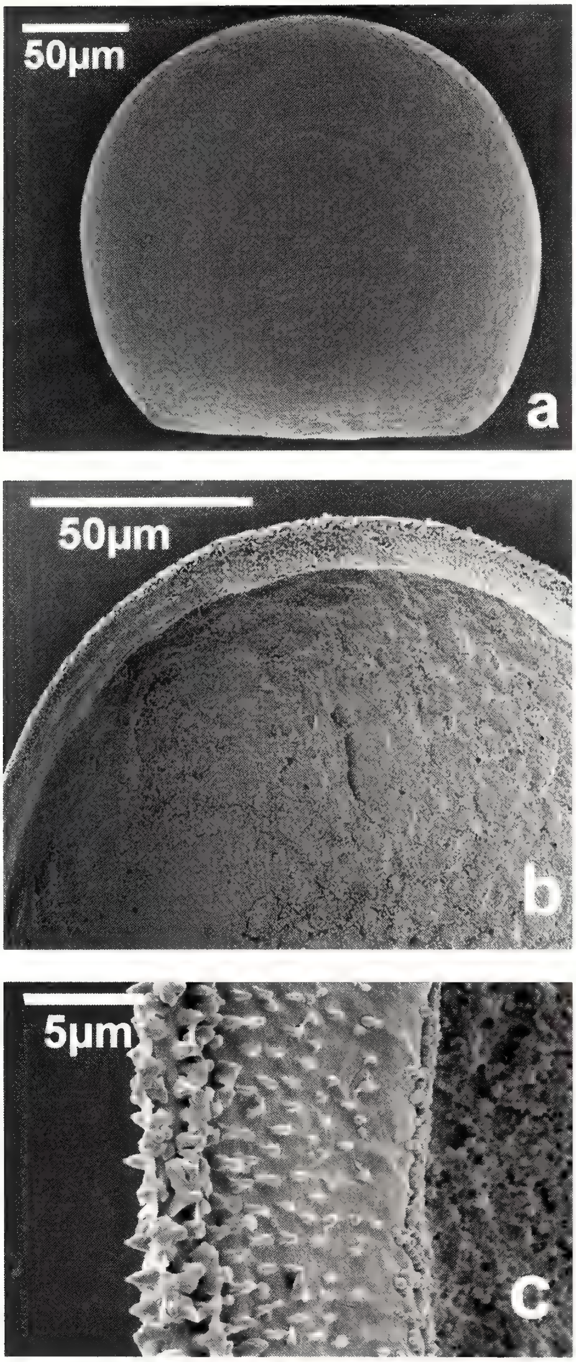

Fig. 2. Scanning electron micrographs of the glochidial shell of *Amblema neislerii*. A. External view of valve. B. Internal view of valve. C. Flange with micropoints.

decrease in number distally (Fig. 2C).

The glochidial valves of *Elliptoideus sloatianus* are depressed and sub-elliptical in shape (Fig. 3A, B). The length of each glochidial valve is 155 ± 12.3 µm (145-170 µm), the height is 139 ± 5.9 µm (130-150 µm), and the straight dorsal margin is 113 ± 8.9 µm (105-130 µm). The ventral margin is curved outward. The shell surface is malleated, and concentric ridges occur over most of the surface. Shell pitting is minimal and shell hooks are absent. The micropoints are lanceolate, in irregular vertical rows, and cover 15% of the flange (Fig. 3C).

The glochidial valves of *Medionidus penicillatus* are depressed and sub-spatulate in shape (Fig. 4A, B). The length of each glochidial valve is 227 ± 6.2 µm (218-241 µm), the height is 290 ± 9.6 µm (280-310 µm), and the straight dorsal margin is 115 ± 5.8 µm (105-129 µm). The ventral margin is curved outward. The shell surface is smooth with minimal pitting and shell hooks are absent. Micropoints are bluntly lanceolate in shape and decrease in size distally (Fig. 4C). There are irregular vertical rows of micropoints that cover about 75% of the flange.

The glochidial valves of *Pleurobema pyriforme* are slightly depressed and sub-elliptical (Fig. 5A, B). The length of each glochidial valve is 168 ± 6.7 µm (155-185 µm), the height is 164 ± 6.0 µm (152-180 µm), and the straight dorsal margin is 128 ± 7.7 µm (120-145 µm). The ventral margin is curved outward and the shell surface is mostly smooth. Slight pitting is apparent on the shell surface and shell hooks are absent. The blunt lanceolate micropoints are arranged in a random fashion covering 25% of the flange (Fig. 5C).

DISCUSSION

Reproductive biology

The tactics used to lure host fish and the identified host fish differed for each of the mussel species. *Amblema neislerii* released glochidia in a white, adhesive web-like mass that indiscriminately wrapped around passing fish when expelled, allowing the glochidia to attach to the fish's fins and gills. The use of a similar adhesive web-like mass has also been described or observed for several other mussel species: *A. plicata* (Say, 1817) (Stein, 1968), *Anodonta cygnea* (Linnaeus, 1758) (Wood, 1974), and *Strophitus subvexus* (Conrad, 1834) (Haag and Warren, 1997). Like other mussel species that have a nonselective approach to attach their glochidia to a potential host fish, *A. neislerii* has a relatively low degree of host specificity.

Elliptoideus sloatianus released rigid conglutinates comprised entirely of undeveloped glochidia in early February in the laboratory. The premature V-shaped conglutinates released by *E. sloatianus* were similar in shape to those described for *Pleurobema collina* (Conrad, 1837) (Hove and Neves, 1994). When the glochidia were mature, the conglutinates of *E. sloatianus* fell apart as soon as they were released. During the host fish experiments, glochidia of *E. sloatianus* were easier to suspend in the water column

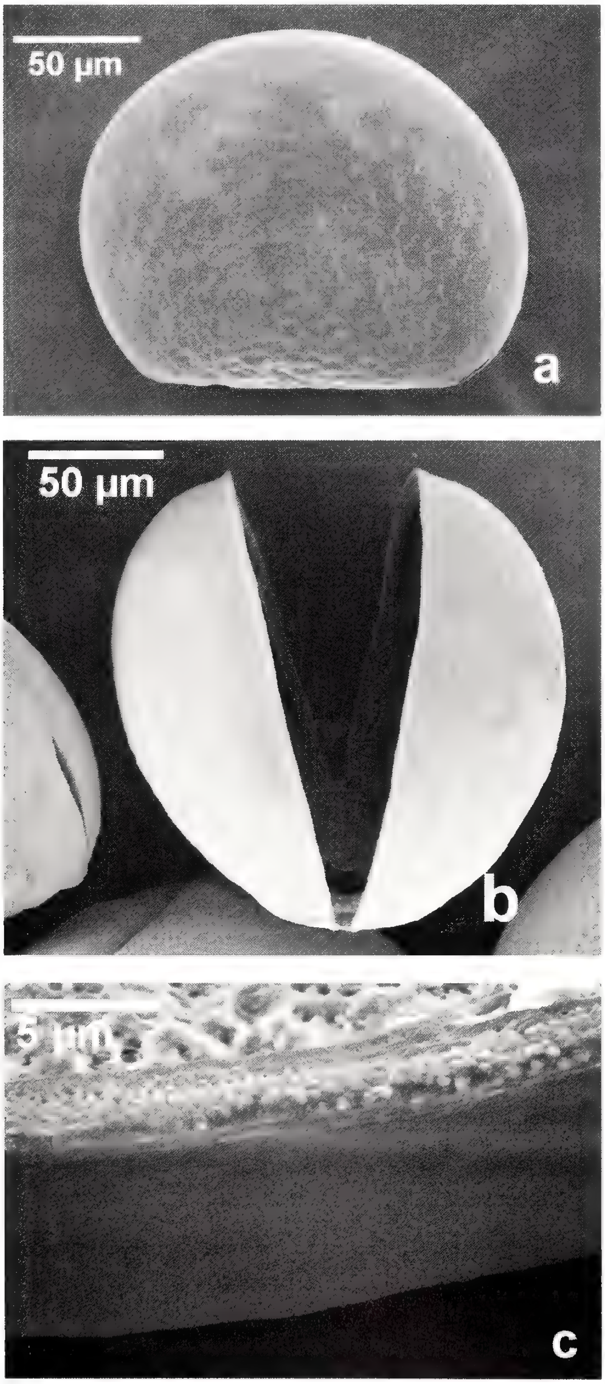

Fig. 3. Scanning electron micrographs of the glochidial shell of *Elliptoideus sloatianus*. A. External view of valve. B. Side view of valves. C. Flange with micropoints.

with aerators compared to the glochidia of other species. This may indicate *E. sloatianus* glochidia rely on stream currents to carry them to a host fish. The primary host fish for *E. sloatianus* remains unknown, indicating it may have a high degree of host fish specificity. The narrow range of suitable host fish and apparent non-selective (i.e. "free" drifting, or adhesive web) mechanism for host fish attachment is perplexing. Freshwater mussels that have a non-selective mechanism to attach to host fish will usually utilize a variety of hosts representing multiple genera (Watters, 1994; Haag and Warren, 1997).

Medionidus penicillatus visually lures its host fish by undulating its dark mantle flaps against swollen white gills. This behavior is also known for other mussels in the subfamily Lampsiline (Kraemer, 1970). Two species of darter (*Etheostoma edwini* and *Percina nigrofasciata*) were identified as primary hosts for *M. penicillatus*. Fishes of the family Percidae have also been identified as the hosts for *M. conradicus* (I. Lea, 1834) (Zale and Neves, 1982) and *M. acutissimus* (I. Lea, 1831) (Haag and Warren, 1997).

Pleurobema pyriforme releases rigid white to pinkish conglutinates with eggs and mature glochidia. Similar conglutinates were described for *P. cordatum* (Rafinesque, 1820) (Yokley, 1972), *P. furvum* (Conrad, 1834) (Haag and Warren, 1997), *P. collina* (Hove and Neves, 1994), and *Fusconaia cuneolus* (I. Lea, 1840) (Bruenderman and Neves, 1993). The release of glochidia via conglutinates is thought to be a mechanism to attract host fish (Haag and Warren, 1997). The conglutinate produced by *P. pyriforme* most likely resembles food organisms utilized by minnows and darters as it drifts passively in the stream current.

Pleurobema pyriforme has a high degree of host specificity. Successful metamorphosis of glochidia occurred on only 3 of the 11 fish species exposed. *Pteronotropis hypselopterus* was the only primary host fish identified for *P. pyriforme*. Other cyprinid fishes have been identified as hosts for *P. cordatum* (Yokley, 1972), *P. oviforme* (Weaver *et al.*, 1991), *P. collina* (Hove and Neves, 1994), and *P. furvum* (Haag and Warren, 1997).

Mussel host specificity ranged from low in *Amblema neislerii* to high in *Elliptoideus sloatianus*. Interestingly, *Gambusia holbrooki* was the only species to successfully metamorphose mussel glochidia on every fish (100%) during the experiment for *E. sloatianus*, but did not produce any juveniles for *A. neislerii*. *Gambusia holbrooki* also served as a host for *Alasmodonta arcula* (I. Lea, 1838), *Elliptio hopetonensis*, *Lampsilis dolabraeformis* (I. Lea, 1838), *Anodontoides radiatus* (C. O'Brien, pers. obs.), and *L. subangulata* (I. Lea, 1840) (O'Brien and Brim Box, 1999). *Poecilia reticulata* also served as a host for *Megalonaias nervosa* (Rafinesque, 1820), *A. radiatus*, *Villosa lienosa* (Conrad, 1834) (C. O'Brien, pers. obs.), *L. subangulata* (O'Brien and Brim Box, 1999), and *Lasmigona compressa* (I. Lea, 1829) (Tompa, 1979). Several researchers have reported fish species from the family Poeciliidae serving as hosts for various North American freshwater mussels (Trdan and Hoeh, 1982; Hove and Neves, 1994; Haag and Warren, 1997; Keller and

Ruessler, 1997; Watters and O'Dee, 1998). However, when fish of the family Poeciliidae were inspected for natural infestation, none were found (Weiss and Layzer, 1995; Roe and Hartfield, 1997). This may indicate that fish species that evolve in areas where mussels are absent or that evolve with native North American mussels, but have very little interaction with the indigenous mussel, lack a natural immunity to their glochidia. However, these data may indicate fish belonging to the family Poeciliidae lack the natural immunity many other fish share.

The role of immunological response to glochidial attachment and host susceptibility varies depending on several factors (e.g. number and frequency of exposure [Bauer, 2001]). Some researchers (Karna and Millemann, 1978; Waller and Mitchell, 1989) suggested that fish resistance to glochidial attachment was a response to the scarring of the gill tissue as a result of repeated glochidial attachments or that the toughness of the tissue discourages a glochidial encystment. Alternatively, Isom and Hudson (1984) and Kirk and Layzer (1997) speculated an immunological response by the fish was responsible for the rejection of the glochidia. It is possible that both of these types of glochidial resistance play a role in the rejection of glochidia.

Many native freshwater mussels evolved elaborate lures as mechanisms to attract specific native host fishes (Coker *et al.*, 1921; Kraemer, 1970; Jansen, 1990; Haag *et al.*, 1995; Hartfield and Butler, 1997; Watters, 1999). If the specific lure also attracts nonindigenous fish that will not complete the mussel's life cycle, reproduction for that mussel species could be reduced. However, the use of nonindigenous fish, which lack immunity to the native North American freshwater mussels, as surrogate host fish could be a useful tool under laboratory conditions when the native host fish is unknown or absent (Watters and O'Dee, 1998).

Glochidial shell morphology

The glochidial shell morphology for these 4 mussel species was consistent with their respective genera. In the past, researchers have used glochidial shell identification to determine periods of glochidial release (Zale and Neves, 1982; Jirka and Neves, 1992) and to confirm laboratory host fish identification with natural infections of glochidia found on fish collected from the wild (Weiss and Layzer, 1995). However, identifying glochidia to the species level can be difficult and almost impossible in streams with a high diversity of unionids that have overlapping periods of glochidial release. Stein (1968) reported the glochidial shell morphology of *Amblema plicata* similar to *Elliptio dilatata* (Rafinesque, 1820). Hoggarth (1999) described the shell shape of *E. dilatata* glochidia as sub-elliptical with size measurements similar to *A. neislerii*. Comparisons of the shell surface and micropoints were not possible, as the

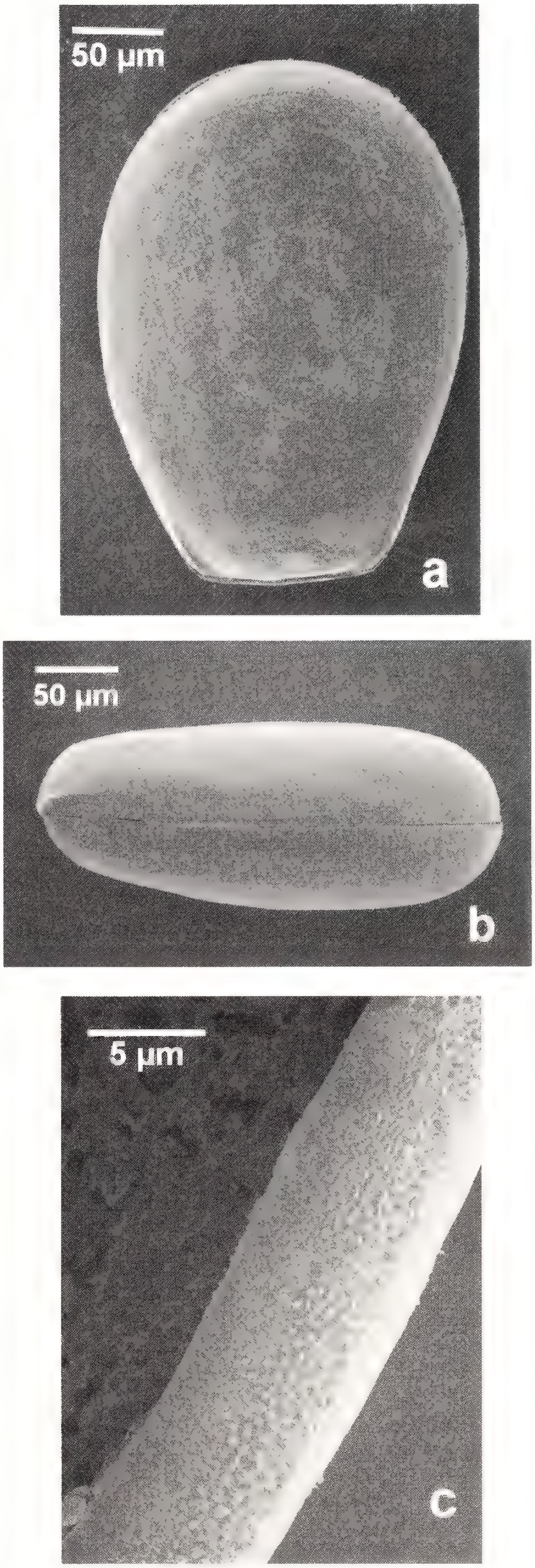

Fig. 4. Scanning electron micrographs of the glochidial shell of *Medionidus penicillatus*. A. External view of valve. B. Side view of valves. C. Flange with micropoints.

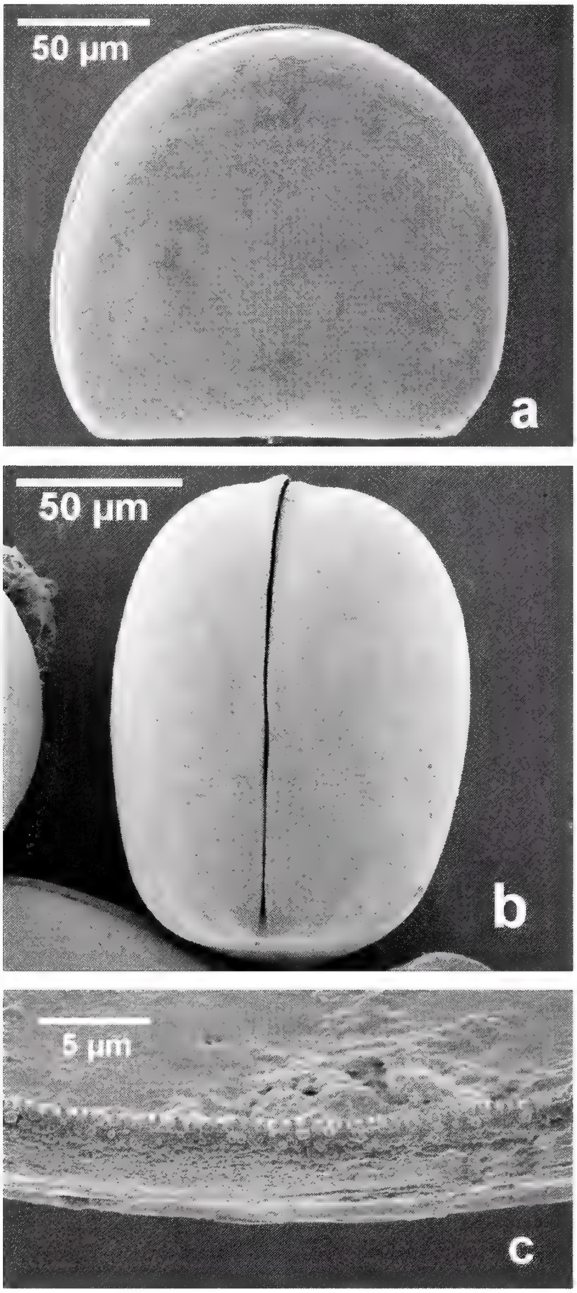

Fig. 5. Scanning electron micrographs of the glochidial shell of *Pleurobema pyriforme*. A. External view of valve. B. Side view of valves. C. Flange with micropoints.

photos of *E. dilatata* did not show enough detail.

The glochidial shell morphology of *Elliptoideus sloatianus* is of special interest because it is a monotypic genus (Turgeon *et al.*, 1998). The depressed sub-elliptical shell shape of *E. sloatianus* appears to be most similar to *Elliptio raveneli* (Conrad, 1834) (Porter and Horn, 1980), *Epioblasma brevidens* (I. Lea, 1831), and *E. capsaeformis* (I. Lea, 1834) (Hoggarth, 1999). However, the glochidial shells of *E. sloatianus* are much smaller. Shell sculpturing found on *E. sloatianus* is similar to the shell surface described for *Epioblasma triquetra* (Rafinesque, 1820) and *E. capsaeformis* (Hoggarth, 1999); however, these species belong to the subfamily Lampsilinae. The sub-spatulate glochidial shell shape of *Medionidus penicillatus* is similar in shape and size of other lampsiline glochidial shells (Ortmann, 1911; Surber, 1912; Porter and Horn, 1980; Waller *et al.*, 1988). The sub-elliptical shell shape and size of *Pleurobema pyriforme* appear to be similar to those of *P. cordatum* (Yokley, 1972). However, the glochidial shells of *P. pyriforme* are about 20 µm (length and width) larger than *P. cordatum* glochidia.

Identifying the species of glochidia attached to fish collected from the wild could be a useful tool to verify laboratory host fish identification. However, this may not be practical in the southeastern U. S. where roughly 90% of the freshwater mussel species occur. The sub-elliptical glochidial shell shapes of *Amblema neislerii* and *Pleurobema pyriforme* could be confused with those of *Elliptio icterina* (Conrad, 1834) and other *Elliptio* spp. (Hoggarth, 1999; O'Brien *et al.*, unpublished) that occur in the Apalachicola, Chattahoochee, Flint, and Ocklockonee river systems (Heard, 1979) and that release glochidia during the same period (Keller and Ruessler, 1997). The shape of the glochidial shells of *Medionidus penicillatus* will be difficult to distinguish from other lampsiline species that have overlapping distributions (Heard, 1979) and periods of glochidial release (Keller and Ruessler, 1997). Based on the glochidial shell morphological information available for a few mussel species, the depressed and sub-elliptical shape of the glochidial shells of *Elliptoideus sloatianus* may be distinctive enough to distinguish them from those of other mussel species in the Apalachicola, Chattahoochee, Flint, and Ochlockonee drainages. The host fish remains unknown for *E. sloatianus*. Therefore the distinctive glochidial shell morphology could be useful in determining the host fish via natural infestations on wild-caught fish.

Efforts to protect endangered and threatened mussel species are greatly improved by gaining vital information about their reproductive biology. Future efforts should focus on investigating the reproductive biology of these imperiled species. Without this basic information, the development of recovery programs will be limited.

ACKNOWLEDGEMENTS

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IN MEMORIAM

Stephen Jay Gould
Tadashige Habe
Donald R. Shasky
R. K. (Dick) Dell
Kikutaro Baba
Hall Haskin

AMERICAN MALACOLOGICAL SOCIETY, INC.
FINANCIAL REPORT

General Accounts

2000 Income and Expenses

TOTAL ASSETS (January 1, 2000)			$179,908.98
INCOME			$ 30,640.85
Membership Dues (1998)		175.00	
Membership Dues (1999)		1,520.00	
Membership Dues (2000)		15,260.00	
Membership Dues (2001)		472.00	
Interest and Dividends		4,947.10	
Money Market Account Interest	1,000.75		
Life Membership Endowment Dividends	258.09		
Symposium and Student Grant Endowment Dividends	3,688.26		
Publications Income		7,196.25	
AMB Foreign Subscriptions	1,331.00		
AMB Domestic Subscriptions	2,352.00		
AMB Page Charges	2,412.00		
AMB Back Issues	550.00		
AMB Reprint Charges	499.50		
Sales of Other Publications	51.75		
Annual Meetings		745.50	
2000 Auction Proceeds	745.50		
Donations		325.00	
Symposium Endowment Fund	125.00		
Student Endowment Fund	200.00		
EXPENSES			$25,021.46
Treasurer Expenses		636.46	
Affiliate Memberships		140.00	
Banking Fees		5.00	
MC - VISA Fees		676.85	
Incorporation and Registration Fees		35.00	
Insurance/Bond Fees		600.00	
Secretary Expenses		145.75	
Publication Expenses		15,514.74	
AMB	7,660.34		
AMS Newsletter and Directory	2,990.94		
Brochures	196.00		
AMS-WSM 2000 Abstracts Printing and Postage	4,667.46		
Student Research Grants		1,920.00	
Meeting Expenses - Separate Accounts			
Travel Expenses		3,847.66	
Bulletin Editor (2000)	1,098.78		
Managing Editor (2000)	1,080.27		
Secretary (2000)	661.00		
Treasurer (2000)	1,007.61		
Student Paper Awards		1,500.00	
NET GAIN IN 2000			$5,619.39
TOTAL ASSETS (December 31, 2000)**			$179,709.49

**Includes capital investments in two endowment portfolios which fluctuate with the market. The above income and expenses does not include the annual meeting accounts.

AMERICAN MALACOLOGICAL SOCIETY, INC.
FINANCIAL REPORT

General Accounts

2001 Income and Expenses

TOTAL ASSETS (January 1, 2001)			$179,908.98
INCOME			$ 22,659.29
Membership Dues (1999)		130.00	
Membership Dues (2000)		551.00	
Membership Dues (2001)		10,538.00	
Membership Dues (2002)		281.00	
Interest and Dividends		4,809.57	
Money Market Account Interest	956.92		
Life Membership Endowment Dividends	163.40		
Symposium and Student Grant Endowment Dividends	3,689.25		
Publications Income		4,654.00	
AMB Foreign Subscriptions	605.00		
AMB Domestic Subscriptions	2,170.00		
AMB Page Charges	525.00		
AMB Back Issues	566.00		
AMB Reprint Charges	786.00		
Sales of Other Publications	2.00		
Donations		1,695.72	
Symposium Endowment Fund	130.00		
Student Endowment Fund	740.00		
American Fisheries Society	825.72		
EXPENSES			$44,607.95
Treasurer Expenses		582.32	
Affiliate Memberships		235.00	
Banking Fees		25.00	
MC - VISA Fees		590.81	
Incorporation and Registration Fees		55.00	
Insurance/Bond Fees		605.00	
Managing Editor Expenses		80.00	
Symposium Speakers		4,260.00	
Publication Expenses		27,529.42	
AMB (15-2, 16-1/2)	27,481.42		
Subscription Refund	48.00		
Student Research Grants		2,000.00	
AMS-WSM Abstract Postage		515.40	
Travel Expenses		3,630.00	
Bulletin Editor (2001)	2,000.00		
Secretary (2001)	1,630.00		
Student Paper Awards		1,500.00	
Student Travel Awards		3,000.00	
NET LOSES IN 2001			$22,446.86
TOTAL ASSETS (December 31, 2001)**			$148,575.42

**Includes capital investment gains and losses in the two endowment portfolios which fluctuate with the market. The above income and expenses also do not include the annual meeting expenses.

American Malacological Society

69th Annual Meeting
Ann Arbor, Michigan
June 25-29, 2003

The 2003 American Malacological Society meeting will be held at the University of Michigan's Central Campus, Ann Arbor, during the last week of June. We hope you can join us for what promises to be an informative and fun conference. In addition to diverse contributed paper and poster sessions, we anticipate the following events:

Symposium I ***Diversification In The Sea - What Can Comparative Molecular Data Tell Us?***
Molecular datasets are providing exciting new insights into the genesis of marine molluscan biodiversity. Invited speakers include Rachel Collin (*Crepidula*), Tom Duda (*Conus*), Michael Hellberg (*Tegul*a), Taehwan Lee (*Brachidontes*), Chris Meyer (Cowries) and Susannah Williams (*Nodolittorina*). Organizer: Diarmaid Ó Foighil (diarmaid@umich.edu).

Symposium II ***Non-Marine Molluscan Exotics - The Future Is A Foreign Ecosystem.***
Until recently, oceanic barriers to dispersal biotically insulated non-marine malacofaunas. The symposium will consider salient case histories illustrating the spread and impact of molluscan exotics in recipient ecosystems. Prospective speakers include Rob Cowie (Pacific Island exotics), Gustavo Darrigran (*Limnoperna fortunei*), Diarmaid Ó Foighil (New World *Corbicula*) and Geerat Vermeij (Pespective on Biological Invasions). Organizer: Rob Cowie (cowie@hawaii.edu).

Special Session I ***PEET Meets Molluscan Taxonomy.***
NSF's PEET program has sponsored a number of significant molluscan taxonomic projects. This special session will highlight the diverse new research emerging from these projects and will facilitate an exchange of information between PEET and the malacological community.
Organizer: Terrence Gosliner (Tgosliner@calacademy.org).

Special Session II ***J.B. Burch - His Students Speak.***
Jack Burch has had a long and influential career in malacology. This special session is in his honor and will feature research presentations, focusing on freshwater and terrestrial molluscs, by his former students. Organizer: Tim Pearce (pearcet@carnegiemuseums.org).

Other projected activities include workshops on Bayesian Phylogenetics and on the use of ROV's in riverine studies, a conchological show and tell session, book auction, a tour of the UMMZ Mollusc Collection and aquatic and terrestrial field trips.

Conference events, accommodation (choice of hotel or college dorm), and social amenities will be within walking distance. Ann Arbor is a culturally lively college town and in late June holds its annual Summer Festival with free nightly outdoor entertainment. See you there!

Diarmaid Ó Foighil, AMS President
UMMZ, University of Michigan, Ann Arbor, MI 48109-1079

For details check out our website at: http://www.ummz.lsa.umich.edu/mollusks/ams2003.html

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CONTRIBUTOR INFORMATION

The *American Malacological Bulletin* serves as an outlet for reporting notable contributions in malacological research. Manuscripts concerning any aspect of original, unpublished research, important short reports, and detailed reviews dealing with molluscs will be considered for publication.

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Hillis, D. M. 1989. Genetic consequences of partial self fertilization on populations of *Liguus fasciatus* (Mollusca: Pulmonata: Bulimulidae). *American Malacological Bulletin* 7:7-12.

Seed, R. 1980. Shell growth and form in the Bivalvia. *In: Skeletal Growth of Aquatic Organisms*, D. C. Rhoads and R. A. Lutz, eds. pp. 23-67. Plenum Press, New York.

Yonge, C. M. and T. E. Thompson. 1976. *Living Marine Molluscs.* William Collins Son and Co., Ltd., London. 288 pp.

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Cover: Synchronized sculptures of some gastropod shells, from Savazzi & Sasaki

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The Southern Plains Gastropod Survey: The distribution of land snail populations in an American grassland environment

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Abstract: The Southern Plains Gastropod Survey represents a quantified baseline survey of terrestrial gastropod assemblages recovered from upland settings along an east to west corridor across the northern portion of the Southern Plains. This 700 km long corridor extends from the Flint Hills of north-central Oklahoma to the foothills of the Rocky Mountains in northeastern New Mexico and crosses three physiographic provinces and four biotic districts. During 1995 and 1996, 13 different locations were sampled for land snails along the corridor, and 117 vegetation detritus samples were collected. These samples produced 35,356 shells assignable to 26 taxa of terrestrial gastropods. The results of this study revealed an east to west shift in the distribution of land snail taxa, with the greatest diversity and density occurring in protected settings that served as catchments for vegetation detritus and moisture. This survey added 55 new county records and 3 new state records of species occurrences.

Key words: land snails, biogeography, Southern Plains, Oklahoma, New Mexico

Although far from North American landscapes that once were covered by glaciers, the Southern Plains have played a prominent role in documenting the effects of late Pleistocene climates and environments. Locations from southwestern Kansas to southwestern Texas have yielded geological and paleontological clues to the diverse environmental settings that developed during different Pleistocene intervals over the past 2 million years (Dalquest 1962, 1965, Hawley *et al.* 1976, Gustavson 1986, Graham 1987, Caran and Baumgardner 1990, Madole *et al.* 1991, Dalquest and Schultz 1992). Archaeological sites in the region also include some of the earliest known for North America and attest to a human presence by 12,000 years ago, and perhaps much earlier (Hofman *et al.* 1989, Bonnichsen and Turnmire 1991, Johnson 1991, Wyckoff *et al.* 1991, Fiedel 1999).

Since the 1950s, geologists, paleontologists, and archaeologists have recognized the importance of gastropods for identifying and correlating Pleistocene deposits on the Southern Plains (Taylor and Hibbard 1955, Hibbard and Taylor 1960, Stephens 1960, Slaughter *et al.* 1962, Taylor 1965, Slaughter 1966, Schultz and Cheatum 1970, Willimon 1972, Devore 1975, Drake 1975, Miller 1975, Wendorf and Hester 1975, Shaak and Franz 1976, Caran *et al.* 1985, Caran and Baumgardner 1990, Wyckoff *et al.* 1991, 1992). Moreover, particular species of snails have been used to help interpret the character of the habitats and environments present when these deposits formed. These interpretations rely on an accurate determination of the geographic distribution of modern snails and the climatic parameters limiting their distribution. Knowledge of modern gastropod species and communities, however, is inadequate (Taylor 1965, Hubricht 1985). Previous gastropod collections have been spotty in coverage, often focusing on compiling lists of species and seldom using a described or comparable sampling or recovery technique (for example, Leonard 1943, Wallen and Dunlap 1953, Branson and Wallen 1955, Hoff 1962, Branson 1972, Neck 1984, Hubricht 1985, Neck 1990). Because some of the recovery methods included shells from "riparian drift," it is possible that reported collections contain mixtures of both modern and Pleistocene specimens (Bequaert and Miller 1973).

To address questions of land snail distributions on the Southern Plains and their potential as proxy indicators of the past, we initiated the present survey in upland settings across the northern border of the region. This project, referred to as the Southern Plains Gastropod Survey (SPGS), concentrated on the collection of terrestrial snails from distinct landforms in these settings. We focused on land snails because of a recognized need for more information on their habitat occurrence on the Southern Plains (Taylor 1965, Neck 1995), and because studies elsewhere have demonstrated that certain species of terrestrial snails can be associated with different habitat parameters (Coney *et al.* 1982, Getz and Uetz 1994).

PHYSICAL SETTING

The SPGS was conducted along a corridor 700 km long and 100 km wide that extends from the Flint Hills of north-central Oklahoma to the eastern margin of the Rocky Mountains in northeastern New Mexico (Fig. 1). This corridor was selected to cross the Southern Plains near a number of localities that have yielded important fossil gastropod assemblages (Taylor 1960, 1965, Hibbard and Taylor 1960, Wells and Stewart 1987). These fossil gastropod assemblages often include terrestrial species that now live in regions to the west or east, where precipitation and temperature regimes are different from those on the Southern Plains today. The SPGS corridor crosses a series of physiographic and biotic regions (Carpenter 1940, Shelford 1963) that link these eastern and western settings. The delineated corridor also provides an opportunity to document the occurrence and abundance of species in a number of distinct landforms in which an array of terrestrial snail species might exist. Finally, the corridor extends across a portion of the Southern Plains where studies of modern gastropods are rare (Leonard 1943, Branson 1972, Metcalf 1984, Metcalf and Smartt 1997).

The SPGS corridor intersects four biotic districts and three physiographic provinces. Although the western terminus was in the foothills of the Rocky Mountains near Cimarron, New Mexico, the majority of the survey was across the two subdivisions of the Southern Plains, the Southern High Plains and the Osage Plains. The physiography and geology of the Southern High Plains and their eroded margin, the Osage or Rolling Plains, have long been recognized as distinctive, especially in terms of Pleistocene deposits, and are well described in the recent literature (Osterkamp *et al.* 1987, Gustavson *et al.* 1991, Madole *et al.* 1991).

The Osage Plains are southeast sloping and range from 455 m above sea level (ASL) in the west to 275 m ASL in the east. They are rolling uplands eroded from soft sedimentary rocks of Permian age (Madole *et al.* 1991). The native vegetation on the Osage Plains at the time of Euro-American contact was predominately a mixture of mid-sized to tall grasses, so this geomorphic area is closely associated with what has been termed the Mixed Grass Plains biotic district (Blair and Hubbell 1938). In the SPGS corridor, notable east-west changes occur in bedrock, precipitation, and vegetation cover, and seven localities in the Osage Plains region were sampled for snails. These localities were 60 to 80 km apart (Fig. 1, Appendix 1).

The Southern High Plains in the western portion of the SPGS corridor fall within the Short Grass Plains biotic district, where the annual precipitation averages 50 cm or less (Blair and Hubbell 1938). The Southern High Plains are almost featureless, with elevations that range from 1220 to 1525 m ASL at their western margin (Gustavson *et al.* 1991). Pockmarked by shallow playas, the plateau's surface is broken only where the Cimarron and Canadian Rivers have incised deep, rugged canyons with sparsely vegetated walls of exposed Permian sandstone and shale overlain by Tertiary-age sand and gravel (Gustavson *et al.* 1991). Three locations were sampled on the Short Grass Plains.

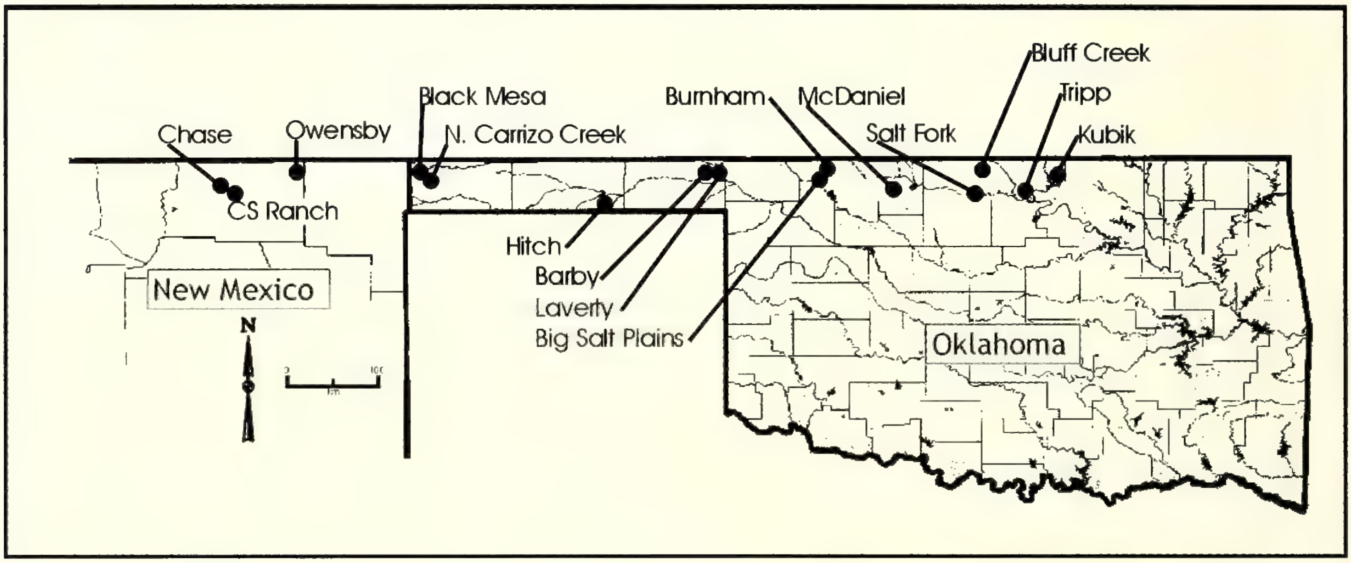

Figure 1. Sampling localities in the Southern Plains Gastropod Survey (SPGS).

The third subdivision sampled is a small, distinctive region characterized today by a biota more like that of the Rocky Mountains than the Southern High Plains. This is the Raton subsection of the High Plains, composed of Miocene and Pleistocene volcano cones, some with crests above 1830 m ASL, and expanses of basalt flows that rest on the Tertiary fluvial deposits. Located in northeastern New Mexico and westernmost Oklahoma, the Raton subsection supports a variety of plants and animals common to the southern Rocky Mountains, the desert Southwest, and the Southern High Plains (Collins 1949, Baldwin and Muehlberger 1959). Two settings were sampled in this region, one at Black Mesa (1465 m ASL) in the northwestern corner of the Oklahoma panhandle, and the other at Johnson Mesa (2255 m ASL), 110 km to the west in northeastern New Mexico.

The SPGS ended at the Chase Ranch in the Rocky Mountain foothills in northeastern New Mexico. The sampling location was at an elevation of 2195 m ASL in the watershed of Ponil Creek, a Canadian River tributary, and was in the dry pine forest community common to these foothills. While not a Southern Plains setting, this last sampled locality offered mountain habitats that support plants similar to those found in the volcanic uplands to the east.

FIELD METHODS

This study was undertaken to document the distribution and abundance of modern species of land snails across the Southern High Plains. Given the need for better information on the biogeography of land snails (Solem 1979), and realizing that we could not adequately sample all the habitats along our corridor, we focused on upland landforms. We avoided alluvial settings because both living and sub-fossil snails are easily redeposited there in riparian drift. However, because riparian woodlands have surfaces littered with decomposing wood and leaves favored by certain terrestrial species (Leonard 1959), we did sample riparian settings along the corridor. At these, we collected from locations above the evident flood "drift" line to avoid redeposited shells. We believe we were successful in this effort; only three aquatic snail shells are represented in our combined samples.

The SPGS sampling procedure did not include hand picking of individual gastropods, a procedure that favors larger-shelled species, the distributions of which are well known. We believed that hand picking would bias our results and prove inconsistent with our survey objectives.

Our collections were taken from what we called *localities.* Each of the 13 localities along the corridor was a setting seldom more than 400 m in diameter. Vegetation, slope, and aspect were important criteria for recognizing distinct landforms at each locality. Each landform was sampled for snails by taking three separate samples along a *transect.* The number of transects at a given locality depended on the number of landforms represented. A transect rarely exceeded 100 m in length, and samples usually were taken at 10 to 20 m intervals. We collected from locations where living snails could be expected, and placed our sample squares where vegetation, humus, and/or vegetation detritus were present. Each sample included the lower parts of living vegetation as well as all vegetation detritus and up to 2 cm of the underlying mineral soil.

The individual 50 x 50 cm sampling squares were designated *a, b,* and *c.* These same designations were given to each series of samples in each transect of a locality. The transects were numbered sequentially during the fieldwork, with each plotted on a U. S. Geological Survey 7.5′ topographic map. A photographic record was made of each sample, transect, and locality. Photographs were placed on file at the Oklahoma Museum of Natural History for future reference. The individual localities and transects are briefly summarized below.

SAMPLE LOCALITIES

Kubic Ranch Locality, Kay County, Oklahoma

Situated in the southwestern part of the Flint Hills, this locality was the easternmost and most mesic of the settings sampled in the SPGS corridor, receiving 86 cm of precipitation annually (Johnson and Duchon 1994). This location is on the modern border between the mixed-grass and tall-grass prairie. Six transects (Nos. 1-6) were undertaken at Kubic, at elevations ranging from 350 to 365 m ASL. The first five transects were along the crest and the north- and south-facing slopes of a limestone-capped mesa that typifies this portion of the Flint Hills. The sixth transect was in a riparian woodland, above recent flood lines, on an intermittent tributary of Beaver Creek, which flows to the Arkansas River.

Tripp Pasture Locality, Kay County, Oklahoma

Transects 7 and 8 were completed on the top and down a gentle south slope of a mixed-grass pasture containing water-holding depressions believed to be former buffalo wallows. At 320 m ASL, this pasture is one of the few uncultivated plots of largely mixed grasses remaining in this portion of the Osage Plains. Today, the vast majority of this gently rolling landscape is planted in wheat.

Bluff Creek Locality, Grant County, Oklahoma

A single transect (No. 36) was taken along a bluff top 0.8 km south of Bluff Creek. The bluff top is at 350 m ASL and is covered with mixed grasses, especially bluestem.

Salt Fork Dunes Locality, Grant County, Oklahoma

An extensive sand dune field parallels the north side of the Salt Fork River. Two transects (Nos. 9 and 10) were completed here, one in a woodland on a dune crest (320 m ASL), and the other in a mixed grass opening along a gentle southeast slope of the dune, about 0.3 km north of the river.

McDaniel Locality, Alfalfa County, Oklahoma

This 1.6-hectare pasture is one of the few uncultivated areas in the west-central portion of the Osage Plains of northern Oklahoma. Located 1.6 km south of the Salt Fork River, this gently sloping pasture is at 375 m ASL. A single east-west transect (No. 11) was taken, with vegetation composed mostly of forbs such as western ironweed and ragweed associated with historic disturbance. The native vegetation would have been predominantly buffalo grass.

Burnham Locality, Woods County, Oklahoma

Five transects (Nos. 12, 13, 14, 16, and 17) were sampled in the mixed grass uplands that form the southern edge of the Red Hills, an eroded High Plains remnant north of the Cimarron River. This region receives 66 cm of annual precipitation (Johnson and Duchon 1994). Four transects were sampled on the crest and the north, south, and west slopes of an uncultivated mesa that is at 610 m ASL. The fifth transect was among juniper and cottonwood trees along a small intermittent tributary to West Moccasin Creek, which drains 6 km south to the Cimarron River.

Big Salt Plains Locality, Woods County, Oklahoma

A single east-west transect (No. 15) was completed through sagebrush and grass along an uncultivated, low sand dune directly north of the Big Salt Plains. This salt flat is on the Cimarron River at an elevation of 480 m ASL.

Skull Springs Locality, Beaver County, Oklahoma

Three transects (Nos. 18-20) were sampled in the vicinity of this historic ranch site. Transect No. 18 was on the Barby property, where short grasses prevailed on uplands at 670 m ASL, at the eastern margin of the Southern High Plains. This area receives 51 cm of precipitation annually (Johnson and Duchon 1994). Transect No. 19, on the A. Laverty property, supported a sparse riparian woodland on a low terrace at 665 m ASL, directly south of the North Canadian River. The last transect, on the R. Laverty property, was along a sagebrush and yucca-covered dune crest at 665 m ASL, 0.4 km north of the North Canadian River.

Hitch Ranch Locality, Texas County, Oklahoma

Three transects were sampled at Hitch, where the annual precipitation is 45 cm (Johnson and Duchon 1994). One transect (No. 21) was across a short-grass and yucca High Plains setting at 930 m ASL, adjacent to the Coldwater Creek valley. A second transect (No. 22) sampled the rocky, grass-covered upper slope at 920 m to 925 m ASL along this valley's south edge. Finally, transect No. 23 was taken in a cottonwood riparian woodland 100 m south of Coldwater Creek's active channel.

Black Mesa Locality, Cimarron County, Oklahoma

Black Mesa forms the eastern edge of the volcanic uplands common over northeastern New Mexico and the adjacent borders of Colorado and Oklahoma. This locale receives 38 cm of annual precipitation (Johnson and Duchon 1994), or less than half of the annual total at Kubic in the Flint Hills, 545 km to the east. Five transects were taken, four of which sampled the mesa crest (No. 24), the north slope (Nos. 25 and 26), and a protected south slope (No. 35) of Black Mesa at 1465 m ASL. This basalt-capped mesa borders the Cimarron River and supports a vegetation community of short bunch grass, yucca, cholla cactus, junipers, and deciduous brush in sheltered areas. A fifth transect (No. 27) was in a willow riparian woodland edge at 1310 m ASL, paralleling North Carrizo Creek 0.8 km north of Black Mesa.

Owensby Locality, Colfax County, New Mexico

Three transects (Nos. 59-61) were taken here in 1996. Transect No. 59 was taken at the southern base of the Johnson Mesa bluff face at 2285 m ASL, and No. 60 was taken along the mesa in Gambel's oak, on a south slope with grasses and pine at 2245 to 2225 m ASL. Transect No. 61 was on top of the mesa in a grove of Gambel's oak at 2316 m ASL.

C. S. Ranch Locality, Colfax County, New Mexico

This westernmost High Plains setting was in the Canadian River basin about 10 km east of the Rocky Mountain foothills. On this ranch, we selected a mesa with yucca, cactus, and grasses at an elevation of 1940 m ASL. The annual precipitation here is 38 cm (National Climatic Center, 1983). At this locality, we sampled the crest with transect No. 28, the north slope with transect No. 29, and the north base with transect No. 30.

Chase Ranch Locality, Colfax County, New Mexico

Located on the Ponil Creek drainage, which flows to the Canadian River, this locality was sampled with four transects in habitats common to the eastern foothills of the southern Rocky Mountains. Three transects (Nos. 31-33) were done at 2225 m ASL on the crest, north slope, and south slope of a pine, oak, grass, and cactus-covered mountain a short distance up Chase Canyon. The other transect (No. 34) was completed in tall grass, forbs, and cottonwoods along an uncultivated portion of the first terrace bordering Ponil Creek's north side.

LABORATORY METHODS

The detritus collected from each of the 117 sample squares was screened through a geologic sieve with a mesh size of 0.425 mm. All complete and potentially identifiable gastropod shell fragments were isolated by searching the processed detritus using a binocular microscope. Only one-half of each sample was analyzed in the seven samples with extremely abundant gastropods: Burnham Transect 12 samples *a* and *c*; Kubic Transect 4 samples *a* and *c*; and Kubic Transect 2 samples *a*, *b*, and *c*. All of the remaining 110 samples were sorted and analyzed in their entirety.

The gastropod shells recovered from each sample were sorted by taxon with reference to Franzen and Leonard (1947), Pilsbry (1946, 1948), Taylor (1960), Burch (1962), and a synoptic collection at the University of Wisconsin-La Crosse. Following identification, the shells were counted and catalogued by taxon. The taxonomic nomenclature used follows Turgeon *et al.* (1998). A series of gastropods recovered during this survey was provided to Dr. Crayton J. Yapp and Ph.D. candidate Meena Balakrishnan at Southern Methodist University in Dallas, Texas, for oxygen and carbon isotope studies. All remaining specimens were deposited at the Field Museum of Natural History, Chicago, Illinois.

During the cataloguing procedure, the individuals of each terrestrial species from each sample were examined to determine whether they were living, fresh, recent, or sub-fossil when collected. This information was then added to the catalogue by species. For the great majority of species recovered, some individuals were found to be living or fresh when collected. An individual was considered "living" if it still contained the soft tissue body of the snail, normally visible through the shell, or if it had an epiphragm. A snail forms an epiphragm under stress of desiccation when the animal withdraws into its shell for estivation and secretes a mucous membrane over the shell aperture to seal in moisture during its dormant state.

A "fresh" shell has no soft tissue or epiphragm but still has the exterior proteinaceous coat, the periostracum. The periostracum is usually destroyed within a year of death (Evans, 1972). When the periostracum is lost, the calcium carbonate that forms most of the shell is exposed to oxidation and generally becomes opaque and white or cream in color. Opaque specimens with an incomplete periostracum were considered "recent." The term "sub-fossil" was reserved for special situations in which a weathered shell seemed out of place and the potential for derivation from redeposited sediments appeared high. Sub-fossil shells did not retain any traces of the periostracum.

RESULTS

The 117 samples taken during the 1995-1996 Southern Plains Gastropod Survey yielded 35,359 gastropod shells (Appendix 2). Three of these shells were of aquatic snail taxa recovered in the riparian woodlands at the Hitch locality in Transect 23 (T-23) and along North Carrizo Creek adjacent to Black Mesa in T-27. The remaining 35,356 shells, excluding juveniles, were assignable to 26 taxa of terrestrial snails. Four weathered shells of three different taxa were recovered from riparian woodlands representing possible redeposited sediments at Hitch, Burnham, and Skull Springs. These shells may have been reworked from Pleistocene or Holocene deposits and are noted as sub-fossils (s.f.) in Appendix 2.

Species Distribution and Abundance

The Southern Plains Gastropod Survey documented a shifting distribution of land snail species along the corridor from the easternmost sampling locality at Kubic to the Chase Ranch 700 km to the west. In this pattern, some species dropped out while others were added to assemblages concomitant with shifts in environmental conditions. The pattern is best illustrated by focusing on the six sampling localities with the largest number of landform types. Significant factors believed to shape the species distributions include sharp decreases in annual precipitation and increases in elevation, with reductions in July temperature and relative humidity (Taylor 1960, Metcalf and Smartt 1997), as one moves west along the corridor (Table 1).

In Oklahoma, our easternmost locality at Kubic produced 17 taxa of land snails, with the next three localities to the west at Burnham, Hitch, and Black Mesa each having 9 or 10 taxa. Gastropod species not found west of Kubic included *Gastrocopta contracta* (Say, 1822), *Gastrocopta pentodon* (Say, 1822), *Euconulus trochulus* (Reinhardt, 1883), and *Millerelix dorfueilliana* (I. Lea, 1838). An additional three species not found west of Kubic in the Oklahoma segment of the corridor were *Gastrocopta holzingeri* (Sterki, 1889), *Gastrocopta armifera* (Say, 1821), and *Glyphyalinia indentata* (Say, 1823). All three of these species, however, were present in eastern New Mexico, and *G. armifera* was located during an earlier survey near the Burnham locality (see Species Discussion).

In the central portion of the corridor at Burnham, Hitch, and Black Mesa, a consistent group of gastropod taxa was represented, including *Gastrocopta procera* (Gould, 1840), *Gastrocopta pellucida* (Pfeiffer, 1841), *Pupoides albilabris* (C. B. Adams, 1841), *Vallonia parvula* Sterki, 1893, *Helicodiscus singleyanus* (Pilsbry, 1889), *Helicodiscus parallelus* (Say, 1817), *Hawaiia minuscula* (A. Binney, 1841), and species of Succineidae.

Table 1. The distribution of land snail taxa (excluding sub-fossils) along the SPGS corridor from east (Kubic) to west (Chase) relative to selected aspects of climate and elevation. Climatic data after Johnson and Duchon (1995) and National Climatic Center (1983). Elevations from USGS 7.5' topographic maps: [1]Hardy, OK-KS; [2]Freedom NW, OK; [3]Guymon SE, OK-TX; [4]Kenton, OK-CO; [5]Trinchera Pass, NM; [6]Cimarron, NM.

State:	Oklahoma				New Mexico	
Collection locality:	Kubic[1]	Barnham[2]	Hitch[3]	Black Mesa[4]	Owensby[5]	Chase[6]
Taxon:	+					
Gastrocopta contracta	+					
Gastrocopta pentodon	+					
Euconulus trochulus	+					
Millerelix dorfueilliana	+					
Helicodiscus nummus	+	+				
Deroceras laeve	+	+	+			
Gastrocopta procera	+	+	+	+		
Pupoides albilabris	+	+	+	+		
Vallonia parvula	+	+	+	+		
Helicodiscus parallelus	+	+	+	+		
Helicodiscus singleyanus	+	+	+	+		
Hawaiia minuscula	+	+	+	+	+	
Succineidae	+	+	+	+		+
Gastrocopta pellucida	+	+		+		+
Gastrocopta holzingeri	+				+	
Gastrocopta armifera	+					+
Glyphyalinia indentata	+					+
Gastrocopta cristata			+			
Pupilla muscorum				+	+	
Vitrina pellucida					+	
Gastrocopta sp.					+	
Euconulus fulvus					+	
Vallonia gracilicosta				+	+	+
Cionella lubrica					+	+
Zonitoides arboreus					+	+
Gastrocopta pilsbryana						+
Annual rainfall (cm)	86	66	45	38	38	38
Elevation (m)	360	650	900	1400	2200	2100
Ave. July Temperature (C°)	28	28	27	26	21	21
Ave. July Relative Humidity (%)	53	45	43	42	40	40

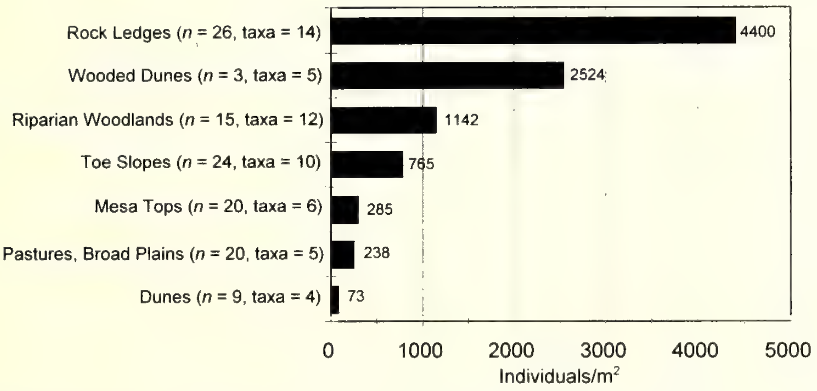

Figure 2. Number of snails per square meter by landform type in the SPGS.

The Black Mesa portion of the Raton subsection at the Oklahoma and New Mexico border is a transitional location for land snail faunas (see Metcalf 1984, Metcalf and Smartt 1997). Sampling at Black Mesa found no species unique to that locality but did yield the westernmost occurrences of *Gastrocopta procera, Pupoides albilabris, Vallonia parvula,* and *Helicodiscus parallelus* and the easternmost appearances of *Pupilla muscorum* (Linnaeus, 1758) and *Vallonia gracilicosta* Reinhardt, 1883. Farther west at the New Mexico localities at Owensby and Chase, the survey recovered several species not found in the Oklahoma samples: *Vitrina pellucida* (Muller, 1774), *Euconulus fulvus* (Muller, 1774), *Cionella lubrica* (Muller, 1774), *Zonitoides arboreus* (Say, 1816), and *Gastrocopta pilsbryana* (Sterki, 1890). *Zonitoides arboreus* was found at Black Mesa during previous surveys (see Species Discussion). Some additional taxa appeared to have more limited distributions, including *Helicodiscus nummus* (Vanatta, 1899), *Deroceras laeve* (Muller, 1774), and *Gastrocopta cristata* (Pilsbry and Vanatta, 1900) (see Appendix 2, Table 1, and Species Discussion).

Another way to examine the influence of habitat on terrestrial gastropods is to look at their diversity in relation to the landform types sampled in the SPGS corridor: dunes, pastures/broad plains, mesa tops, toe slopes, riparian woodlands, wooded dunes, and rock ledges. The greatest diversity of snail species was found in the protected setting of rock ledges, followed by riparian woodlands and toe slopes. The lowest diversity was found in the driest and most physically stressed settings: pastures, mesa tops with thin soil cover, and excessively well-drained dunes (Fig. 2, Table 2).

In general, the most protected and moist habitats produced the most snails per square meter. The rock ledges at Kubic, Burnham, and Black Mesa yielded numerous snails. Overall, the SPGS rock ledges, with 26 samples, produced a density of 4,400 individuals/m^2. This landform was followed by riparian woodland areas such as those at Kubic, N. Carrizo Creek adjacent to Black Mesa, and Hitch, with 15 samples yielding a mean of 1,142 individuals/m^2. The portion of the Salt Fork dune that supports an old growth woodland represented a unique habitat in our survey, with a low species diversity but a high density of individuals. This habitat has a thick layer of vegetation detritus, which probably affects gastropod density, as suggested by Transect 9, where snails occurred at a density of 2,525 individuals/m^2, compared to the density of 31 individuals/ m^2 on an adjacent, open, grass-covered area on the same dune in Transect 10 (Appendix 2, Table 2).

The driest, least protected sites supported both the lowest species diversity and the lowest densities of snails. An excellent example is the Kubic locality, where Transect 2 at the well-vegetated, protected rock ledge at the mesa margin had a density of 7,312 individuals/m^2, in contrast to Transect 3 on top of the same mesa, where thin soil and vegetation lay immediately on caprock, and the density of snails was only 115 individuals/m^2 (Appendix 2).

New County and State Records

The gastropod species recovered during the SPGS were compared by county to the distribution records shown by Hubricht (1985). A total of 55 new county records and 3 state records were established by the SPGS (Table 3). The relatively large number of new county records reflects a lack of previous surveys for land snails in this portion of the Southern Plains.

Table 2. Landforms sampled at SPGS localities with total number of land snail taxa and mean number of shells per square meter. Key to Landforms: D = dunes; MT = mesa tops; PB = pastures, broad plains; RL = rock ledges; RW = riparian woodlands; TS = toe slopes; WD = wooded dunes.

Locality	Landforms Sampled	Total Number of LandSnail Taxa	Mean Number of Land Snails per m^2
Chase	MT, RW, RL	8	228
C.S. Ranch	MT, TS	4	92
Owensby	PB, MT, TS, RL	9	336
Black Mesa	MT, TS, RW, RL	10	2937
Hitch	MT, TS, RW	9	1301
Skull Springs	D, PB	6	452
Big Salt Plain	D	4	157
Burnham	MT, TS, RW, RL	10	4763
McDaniel	PB	2	49
Salt Fork	D, WD	5	1277
Bluff Creek	PB	5	273
Tripp	PB	4	13
Kubic	MT, TS, RW, RL	17	2505

Gastropod Rank Order

The rank order and assemblage frequency for each species was calculated for the summed terrestrial gastropods from the 117 samples in the SPGS. The number of occurrences for each species in the 117 samples was chosen as the ranking criterion. The number of transect occurrences followed the number of occurrences in the samples, with only two exceptions. The percent of individuals of each species recovered during the survey was calculated, with results at some variance with sample ranking (Table 3).

Table 3. Rank order and frequency of summed terrestrial gastropods from 117 samples and 39 transects in the SPGS. *Recovered in E. New Mexico samples only.

		Number of Occurrences					
Taxon	Rank	Samples	Transects	Number of Specimens	Percent of Specimens	Number of New County Records in Oklahoma	New Oklahoma Record
Pupoides albilabris	1	77	31	611	3.0	5	
Gastrocopta procera	2	67	26	4897	24.2	7	
Gastrocopta pellucida	3	47	18	5980	29.5	4	
Hawaiia minuscula	4	43	23	745	3.7	6	
Succineidae	5	32	17	487	2.4	0	
Helicodiscus singleyanus	6	27	13	187	0.9	7	X
Helicodiscus parallelus	7	25	13	355	1.8	5	
Vallonia parvula	8	23	9	1474	7.3	5	
Vallonia gracilicosta	9	21	9	2406	11.9	0	
Helicodiscus nummus	10	20	9	263	1.3	2	X
Glyphyalinia indentata	11	17	7	145	0.7	0	
Gastrocopta armifera	12	15	6	137	0.7	3	
Gastrocopta contracta	13	14	5	511	2.5	1	
Deroceras laeve	14	11	8	22	0.1	3	
Pupilla muscorum	14	11	5	689	3.4	1	X
Gastrocopta cristata	15	8	4	652	3.2	3	
Zonitoides arboreus	15	8	4	97	0.5	0	
Millerelix dorfueilliana	15	8	3	37	0.2	0	
Cionella lubrica	16	6	3	88	0.4	0*	
Euconulus fulvus	16	6	3	17	0.1	1	
Gastrocopta pilsbryana	16	6	2	236	1.2	0*	
Gastrocopta holzingeri	17	5	3	108	0.5	1	
Vitrina pellucida	18	3	2	42	0.2	0*	
Gastrocopta pentodon	18	3	1	38	0.2	1	
Gastrocopta sp.	19	1	1	21	0.1	0*	
Euconulus trochulus	19	1	1	18	0.1	0	
Subtotals				20263	101.1	55	
Vallonia sp.		41	17	6413			
Millerelix sp.		8	3	128			
Juveniles = Terrestrial Taxa				8548			
Aquatic Snails		3	2	3			
Subtotal				15092			
Excluded Subfossil Shells		3	3	4			
Total				35359			

SPECIES DISCUSSION

The following discussion presents the species in rank order, according to the number of samples in which they were found (Table 3), and if those were equal, by the number of transects in which they were found, and then by the number of specimens. A listing of species in taxonomic order following Turgeon *et al.* (1998) is presented in Appendix 2.

Pupoides albilabris

The most widespread species, ranking 1st in occurrence in the SPGS, was *P. albilabris,* represented in 77 of the 117 samples and 31 of the 39 transects. The total number of individuals was low, with 611 specimens recovered, or 3.0% of the 20,263 specifically identifiable terrestrial gastropods. *Pupoides albilabris* was found on all landform types. It is renowned as one of the most xeric-tolerant species on the Plains (Leonard 1959).

The preferred habitat of *Pupoides albilabris* is reported to be among the roots of prairie grasses, on exposed limestone bluffs and ledges, or on dry, open wooded hillsides (Leonard and Goble 1952, Fitch and Lokke 1956, Branson 1960, Basch *et al.* 1961, Bequaert and Miller 1973). *Pupoides albilabris* is infrequently reported from moist, sheltered woodlands.

Gastrocopta procera

This species ranked 2nd in occurrence and was found in 67 of 117 samples from 26 transects. The 4,897 specimens represented 24.2% of the specifically identifiable gastropods. *Gastrocopta procera* occurred at all landform types but was most abundant at rock ledges and toe slopes and least common at dune habitats.

The reported habitat associations for *Gastrocopta procera* indicate that it is most abundant on prairie hill slopes, where it lives among grass roots, or on well-drained, open, woodland hillsides, under debris that provides some protection. In moister habitats, *G. procera* is uncommon or absent (Leonard and Goble 1952, Basch *et al.* 1961, Cheatum and Fullington 1973). The distribution of this taxon is decidedly southern (Reigle 1963, Theler 1997); it appears to be limited in its distribution by the length of the growing season, and does not live in regions with fewer than approximately 160 frost-free days (Baerreis 1980). The westernmost occurrence of *G. procera* was at the Black Mesa locality in Cimarron County, Oklahoma. The absence of this species from the Owensby, C. S. Ranch, and Chase localities, all of which have growing seasons shorter than 160 days, is consistent with this observation.

Gastrocopta pellucida

This species ranked 3rd in occurrence and was found in 47 samples from 18 transects. The 5,980 individuals represented 29.5% of all the identifiable gastropods in the SPGS, making it the most abundant species. The distribution of *G. pellucida* by landform type was distinct. On the mesa top landform, *G. pellucida* was recovered in Transect 13 at the Burnham locality, but at none of the other five mesa-top transects. In addition, the number of *G. procera* recovered at Burnham T-13 marked this mesa-top habitat as distinct from the other five sampled. This distinctiveness may be attributed to a relatively thick soil cover on the Burnham mesa top and associated dense stands of grasses that provide an exceptional, protected habitat.

Gastrocopta pellucida was most abundant at the rock ledges, where it had a density of 1,168 individuals/m^2. This species occurred at all rock ledges in our survey, except at the westernmost Chase and Owensby localities. At riparian woodlands, this species was found both at North Carrizo Creek adjacent to Black Mesa, and at Burnham, with an average density of 249 individuals /m^2, but was absent at Kubic and represented only by one weathered sub-fossil shell at Hitch. Small numbers of *G. pellucida* were recovered on toe slopes at four of the five sampled localities. Given the abundance of *G. pellucida* at the Kubic rock ledges, its near absence at the adjacent toe slope of Kubic Transects 1 and 5 is remarkable. Its sparse occurrence and the absence of living individuals at these Kubic toe slopes might indicate downhill "drift" rather than viable populations. This species appears to be nearing its northern range margin at Kubic (Hubricht, 1985) and may require a protected habitat to survive. *G. pellucida* was not found in the pasture/broad plain settings. It did occur in some numbers at dunes (68 individuals/m^2) and was very abundant (408 individuals/m^2) at the wooded dune at the Salt Fork locality, T-10. This species was found as far west as the C. S. Ranch locality in Colfax County, New Mexico, but was not recovered at the higher elevations at the Owensby or Chase localities to the west of C. S. Ranch, in the same county.

Hawaiia minuscula

Ranking 4th in occurrence was *Hawaiia minuscula,* recovered in 43 samples from 23 transects, with a total of 745 individuals representing 3.7% of all the identifiable snails. This species did not occur at the Chase, Big Salt Plain, or McDaniel localities and occurred in very low density at C. S. Ranch, Skull Springs, and Bluff Creek. *Hawaiia minuscula* had a moderate density at the rock ledges at the Black Mesa, Burnham, and Kubic localities. The highest densities were at the Hitch locality, in a protected rocky, grass-covered habitat on the toe slope of T-22/S-*a*, and under downed cottonwood limbs/debris in the riparian woodland of T-23/S-*a*. The relative rarity or absence of this species in other samples from these transects probably indicates the influence of microhabitat conditions on the abundance of this taxon. Individuals of *H. minuscula* were relatively easy to separate from the similar *Helicodiscus singleyanus* by the slightly higher spires covered with distinct striae on the upper shell surface.

Succineidae

The Succineidae, which ranked 5th in occurrence, were found in 32 samples from 17 transects, with a total of 487 individuals representing 2.4% of all the identified snails. Genera and species of Succineidae are not readily distinguishable by shell characteristics (Leonard 1959, Wu 1993), and no attempt was made to determine species for the individuals of this taxon recovered in the SPGS. No clear differences in shell form were observed. The rocky microhabitat at Hitch T-22/S-*a* yielded 184 of the 487 individuals, or 38% of all the Succineidae recovered. In general, individuals of this family were widespread and somewhat sporadic in occurrence. This family was represented at all landforms except the wooded dune T-10 at the Salt Fork locality.

Helicodiscus singleyanus

This species, which ranked 6th in occurrence, was present in 27 samples from 13 transects. Its 187 individuals represented 0.9% of the identifiable snails. This species did not occur at the Chase, C. S. Ranch, Owensby, Big Salt Plain, Salt Fork, or Tripp localities. The highest densities were at a mesa top (Black Mesa T-24, with a density of 83 individuals/m^2) and 5 of 8 rock ledges, where it had a density of 62 individuals/m^2. It was found in the riparian woodlands at Black Mesa, Hitch, Burnham, and Kubic, with a density of 17 individuals/m^2. The occurrences of this taxon on toe slopes are represented by 3 individuals in a single Black Mesa sample, T-26/S-*c*. On pastures/broad plains, *H. singleyanus* was found in low numbers at the Bluff Creek and Skull Springs localities and was absent from dune settings. This species may be consistently separated from *Hawaiia minuscula* by the lower spire and smoother shell surface.

Helicodiscus parallelus

Ranked 7th, *Helicodiscus parallelus* occurred in 25 samples from 13 transects, with a total of 355 individuals representing 1.8% of all the identified snails. This species was not recovered at the Chase, C. S. Ranch, Owensby, or Big Salt Plain localities. The westernmost location was at Black Mesa in Cimarron County, Oklahoma. It was present at most rock ledges (except at Chase, Owensby, and Black Mesa), with a density of 139 individuals/m^2. Except at Chase, it was also found in all riparian woodlands, with a density of 31 individuals/m^2; however, this figure was inflated by the large number (n = 38) found at Hitch T-23/S-*a*. Toe slopes produced only 2 individuals at Burnham T-16. The number of *H. parallelus* found at the Kubic rock ledges (n = 267, or 75% of all *H. parallelus*) stands in sharp contrast to the complete absence of this species on the toe slopes immediately below the rock ledges, a situation similar to the distribution of *Gastrocopta pellucida* at Kubic. One *H. parallelus* was recovered in a pasture/broad plain sample, and no specimens occurred on dunes.

Vallonia parvula

Vallonia parvula ranked 8th in the SPGS, with occurrences in 23 samples from 9 transects. The 1,474 individuals of this species represented 7.3% of all the identifiable specimens. *Vallonia parvula* was not recovered at the Chase, C. S. Ranch, Owensby, Skull Springs, Big Salt Plain, McDaniel, Bluff Creek, or Tripp localities. No individuals of this species came from mesa top or pasture/broad plain landforms. The highest density of *V. parvula* occurred on the wooded dune at the Salt Fork locality, where 562 individuals (representing 38% of all *V. parvula*) were found in T-9/S-*a*, *b*, and *c* at a density of 749 individuals/m^2. The open prairie (T-10) adjacent to T-9 was sampled, and only 4 individuals of *V. parvula* were recovered, pointing again (as noted above for *Gastrocopta pellucida* and *Helicodiscus parallelus*) to the effects of microhabitat on the abundance and distribution of gastropod communities.

Three of the 10 rock ledges yielded 762 individuals (representing 52% of all *Vallonia parvula*). This species was found at the riparian woodlands at Black Mesa, Hitch, and Kubic at a low density of 67 individuals/m^2. Toe slope occurrences were restricted to T-5 at Kubic, where the density was 39 individuals/m^2.

On wooded, hilly land of the University of Kansas Natural History Reservation in Douglas County, Kansas, Leonard and Goble (1952) found *Vallonia parvula* most abundant on dry, steep, thickly wooded south- and west-facing slopes, and in lower numbers in moister settings. Basch *et al.* (1961) did not find *V. parvula* in prairie or other extremely dry habitats on the Ross Natural History Reservation in east-central Kansas, but did recover it in vegetation detritus associated with hedgerows. Taylor (1960) found *V. parvula* in northern Nebraska under stones, logs, and bark in wooded areas.

Vallonia gracilicosta

Vallonia gracilicosta ranked 9th and was present in 21 samples from 9 transects. The 2,406 individuals of this species represented 11.9% of all identified snails. This species occurred at the western end of the transect at the Chase, Owensby, and Black Mesa localities. The highest density was at the rock ledges, where the density was 1,268 individuals/m^2.

It was also found in riparian woodlands at a density of 238 individuals/m^2, on toe slopes at a density of 134 individuals/m^2, in a mesa-top sample at Chase (T-32/S-*c*) at a density of 96 individuals/m^2, and at Owensby (T-61/S-*b* and *c*) at a density of 24 individuals/m^2.

This species is characteristically associated with cool-episode Pleistocene deposits on the Southern High Plains. Its occurrence in viable populations as far east as Black Mesa appears to represent a disjunct population. It is more typically found today in the eastern foothills of the Rocky Mountains, with the Chase locality representing such a case (Metcalf 1984, Metcalf and Smartt 1997).

Helicodiscus nummus

Helicodiscus nummus ranked 10th, with occurrences in 20 samples from 9 transects. Its 263 individuals represented 1.3% of the identified snails. *Helicodiscus nummus* was found only at the Burnham (n = 158) and Kubic (n = 105) localities, and they appear to be disjunct populations. The most common associations were rock ledges, at a density of 110 individuals/m^2. Next were mesa tops, with one transect at Burnham having a density of 27 individuals/m^2, and then toe slopes, with 2 of 7 transects represented at a density of 20 individuals/m^2.

Glyphyalinia indentata

Glyphyalinia indentata, which ranked 11th, was present in 17 samples from 7 transects, with 145 snails representing 0.7% of the identified specimens. Five *G. indentata* were recovered at the Chase locality; the remaining 140 individuals were recovered at the Kubic locality. At Kubic this species was found on all landforms, with most individuals coming from riparian woodlands (at a density of 68 individuals/m^2), rock ledges (58 individuals/m^2), toe slopes (31 individuals/m^2), and mesa tops (4 individuals/m^2). This species is widespread in the east and is at its western range margin on the Great Plains at Kubic (Hubricht 1985). The species is widespread at higher elevations in New Mexico (Metcalf and Smartt 1997).

Gastrocopta armifera

Gastrocopta armifera ranked 12th, with occurrences in 15 samples from 6 transects, and 137 individuals representing 0.7 % of the identified terrestrial snails. One individual was recovered from the Chase riparian woodland (T-34/S-*a*), while 6 individuals came from Salt Fork T-9, and the other 130 specimens were found at Kubic. The two Kubic landforms represented were the rock ledges, with a density of 127 individuals/m^2, and the adjacent toe slopes, with a density of 17 individuals/m^2. No *G. armifera* were recovered during the 1995 sampling at the Burnham locality; however, in 1990 a population of this species was found in a sample taken by J. L. Theler under mesa caprock near the Burnham locality.

Gastrocopta contracta

Gastrocopta contracta ranked 13th, occurring in 14 samples in 5 transects, with 511 individuals making up 2.5% of all identifiable specimens. This species was recovered only at the Kubic locality, where it appears to be at the western fringe of its range on the Great Plains (Leonard 1959, Hubricht 1985). At the Kubic rock ledge, *G. contracta* had a density of 505 individuals/m^2. The species was present in the riparian woodlands at Kubic (T-6), where its density was 68 individuals/m^2, and on the toe slopes, where its density was 52 individuals/m^2. This eastern species appears to reach its western range limit on upland landforms at circa 81 to 88 cm of annual precipitation.

Deroceras laeve

Deroceras laeve is the only native slug species widespread across the Great Plains (Hubricht 1985). This species was identified by its distinct scale-like internal shell. The specimens recovered are entirely consistent in size and morphology to those of *D. laeve.* This species was not observed living, but the fresh appearance of many of the shells indicated that it has viable populations in the areas sampled. On a cautionary note, a number of European slug species with similar internal shells have been introduced into North America. They typically are associated with urban settings such as greenhouses, lawns, gardens, and damp basements (Pilsbry 1948, Leonard 1959, Bequaert and Miller 1973, Metcalf and Smartt 1997). The SPGS was careful to sample in rural, natural settings where introduced snail species would be unlikely to occur.

Deroceras laeve was one of two species ranked 14th, with occurrences in 11 samples and 8 transects. The 22 specimens represented 0.1% of the identified snails. This species did not occur in the SPGS localities of Chase, C. S. Ranch, Owensby, Black Mesa, Skull Springs, Big Salt Plain, or Bluff Creek. It did not occur on the mesa top or dune landforms. It was most common, in decreasing frequency, at riparian woodlands, toe slopes, rock ledges, and pastures/broad plains.

Pupilla muscorum

Pupilla muscorum shared the 14th ranking and also occurred in 11 samples, but in only 5 transects. Its total of 689 individuals formed 3.4% of the identified snails. *Pupilla muscorum* was recovered at the Black Mesa rock ledge, where it had a density of 395 individuals/m^2. It was also represented at the Owensby locality, west of Black Mesa. At Owensby, this species had a density of 164 individuals/m^2 in rock ledge sample T-59/S-*a*, and 20 individuals/m^2 in the toe slope and mesa top samples. This species, like *Vallonia gracilicosta,* has disjunct populations (Bequaert and Miller 1973) marking exceptional microhabitat outliers on the eastern margins of the species' modern range

(Metcalf 1984). In North America, *P. muscorum* is found in assemblages deposited on the Southern High Plains during the cooler phases of the Pleistocene (Taylor 1965, Hubricht 1985).

Gastrocopta cristata

Gastrocopta cristata was the first of three species ranked 15th and was found in 8 samples from 4 transects, its 652 individuals representing 3.2% of the identified gastropods. *Gastrocopta cristata* was found at the Big Salt Plain ($n = 2$), Skull Springs ($n = 68$), and Hitch ($n = 582$) localities, with 98% recovered from the Hitch riparian woodlands of T-23, where the density was 776 individuals/m^2. Other landforms with *G. cristata* included pastures/broad plains (89 individuals/m^2) and dunes (6 individuals/m^2). *Gastrocopta cristata* did not occur in the mesa top, rock ledge, toe slope, or wooded dune samples.

Gastrocopta cristata was recovered at the Big Salt Plain locality in Woods County, Oklahoma, an occurrence that marks the eastern margin of its range. It was also recovered in Beaver County (Skull Springs) and Texas County, Oklahoma (Hitch). When these new records are added to the *G. cristata* records for Harper and Cimarron Counties, Oklahoma, shown by Hubricht (1985), a continuous distribution is indicated for the five northwestern counties in Oklahoma. According to Hubricht's (1985) map, the northern margin for this species is represented by occurrences in Morton and Meade Counties, Kansas, which are adjacent to Beaver and Texas Counties. However, the Kansas distribution given by Leonard (1959), while indicating an eastern boundary similar to that noted by Hubricht and the SPGS, shows a statewide spotty distribution to the west and north not shown by Hubricht (1985).

Zonitoides arboreus

Sharing the 15th ranking was *Zonitoides arboreus*, also with occurrences in 8 samples and 4 transects, but with only 97 individuals representing 0.5% of the identified specimens. *Zonitoides arboreus* was found at the Chase and Owensby localities. In the Chase mesa top sample, it had a density of 44 individuals/m^2. In 5 samples at 2 rock ledges, its density was 49 individuals/m^2. At Owensby, *Z. arboreus* was represented at rock ledge T-59/S-*a* at a density of 12 individuals/m^2, and at toe slope T-59/S-*b* at a density of 8 individuals/m^2. This species was found living by J. L. Theler in voids of north-facing basalt talus slope at Black Mesa in Cimarron County, Oklahoma, during 1992, and earlier by Metcalf (1984), but was not found during the 1995 SPGS sampling in the same area.

Millerelix dorfueilliana

The third species sharing the 15th ranking was *Millerelix dorfueilliana*, found in 8 samples but only 3 transects. The 37 individuals represented 0.2% of the total identifiable specimens. *Millerelix dorfueilliana* was restricted to the Kubic rock ledge samples, where it had a density of 23 individuals/m^2. In the Kubic riparian woodlands, its density was 4 individuals/m^2. *Millerelix dorfueilliana* is at its western range limit at the Kubic locality (Branson 1962, Hubricht 1985).

Cionella lubrica

The first of 3 species sharing the 16th ranking was *Cionella lubrica*, with occurrences in 6 samples from 3 transects. The 88 individuals represented 0.4% of the identified snails. This species occurred at the Chase locality, in the rock ledge (62 individuals/m^2), riparian woodland (8 individuals/m^2), and mesa top (4 individuals/m^2) samples. *Cionella lubrica* was also recovered at the Owensby rock ledge (T-59/S-*a*) at a density of 76 individuals/m^2 and the Owensby oak woodland toe slope (T-59/S-*b*) at a density of 20 individuals/m^2.

Euconulus fulvus

Euconulus fulvus also ranked 16th, occurring in 6 samples from 3 transects at the Owensby locality. It occurred in relatively low numbers, with a total of only 17 individuals, at the rock ledge, mesa top, and toe slope landforms. Hubricht (1985) notes that this species is not found on the Great Plains west of east-central Iowa. Metcalf and Smartt (1997) observe that this species is common in the forested mountains of New Mexico, and they list it as occurring in Colfax County.

Gastrocopta pilsbryana

Gastrocopta pilsbryana was the third species sharing the 16th ranking, occurring in 6 samples but only 2 transects. Its 236 individuals constituted 1.2% of the identified assemblage. This species was recovered only at the rock ledges at Chase, where its density was 156 individuals/m^2. Pilsbry (1948) states that *G. pilsbryana* is one of the most common species on mountains or plateaus over 1219 m in elevation in both New Mexico and Arizona.

Gastrocopta holzingeri

Gastrocopta holzingeri ranked 17th, with occurrences in 5 samples from 3 transects. With a total of 108 individuals, this species represented 0.5% of the identified assemblage. *Gastrocopta holzingeri* was found at the Kubic locality, where it was most numerous (112 individuals/m^2) at rock ledge T-2/S-*b*. The Kubic occurrence of *G. holzingeri* is consistent with the western range margin in upland settings. The presence of this species at the Owensby locality in Colfax County, New Mexico, may represent a distinct population along the eastern slope of the Sangre de Cristo Mountains, as indicated by

Metcalf and Smartt (1997), who list *G. holzingeri* in adjacent Union, Mora, and Santa Fe Counties. Leonard (1959) indicates that this species is widespread over northern Kansas. The distribution of this taxon in Oklahoma as shown by Hubricht (1985) is inconsistent with our findings in upland settings.

Vitrina pellucida

Vitrina pellucida was one of two species ranked 18th, occurring in 3 samples from 2 transects at the Owensby locality. Only 42 individuals were found, representing 0.2% of the identifiable specimens. This species was most abundant at rock ledge T-59/S-*a*, with a density of 92 individuals/m^2. It also occurred on the toe slopes, with a density of 21 individuals/m^2. *Vitrina pellucida* is a species typical of the eastern Rocky Mountains, where it is usually found in the cooler life zone above 2440 m ASL. It has been recorded for Colfax County by Pilsbry (1946) as well as by Metcalf and Smartt (1997).

Gastrocopta pentodon

Gastrocopta pentodon was the second species sharing the 18th ranking, with occurrences in 3 samples but only 1 transect. A total of 38 individuals represented 0.2% of the total assemblage. Living *G. pentodon* were found at the Kubic locality, where they occurred in the riparian woodlands. The density of *G. pentodon* at Kubic was 51 individuals/m^2. Two sub-fossil shells were recovered, one each at the Hitch and Skull Springs localities. These weathered specimens are likely to have been reworked from older sediments rather than representing modern populations in these areas. At Kubic, *G. pentodon* is on the western edge of its range in upland settings on the Great Plains.

Gastrocopta new species?

Sharing the 19th ranking was a form of *Gastrocopta* found in only 1 sample from 1 transect. At the Owensby rock ledge (T59/S-*a*), a total of 21 gastropod shells had an exterior shell morphology similar to that of *Gastrocopta holzingeri.* The apertural teeth of these individuals, however, were different from those of *G. holzingeri,* which also occurred in this sample. These unusual specimens were examined by Drs. Arthur E. Bogan and Artie L. Metcalf, who did not recognize them as a described species and suggested the possibility of a phenotypic variation of *G. holzingeri.* An attempt to locate another population in the same region was undertaken during July 1998. Sampling on the north face of Johnson Mesa 1.6 km from the T-59/S-*a* sample, which was taken on a southern exposure of the same mesa, uncovered this distinct form of *Gastrocopta* in large numbers, with no examples of *G. holzingeri.* Pending the final results of the 1998 sampling in the Johnson Mesa area of Colfax County, these individuals might be described as a new species.

Euconulus trochulus

The other species ranked 19th was *Euconulus trochulus,* with an occurrence in 1 sample of 1 transect and only 18 individuals recovered (0.1% of the identified specimens). These individuals were found at the Kubic locality on the riparian woodland and had a density of 72 individuals/m^2. This species occurs in the southeastern United States; the Kay County, Oklahoma, occurrences at Kubic mark this species' northwest range extreme in the Oklahoma-Kansas area (Hubricht, 1985).

DISCUSSION AND CONCLUSIONS

The 1995-1996 Southern Plains Gastropod Survey provides a quantified database of terrestrial gastropod populations along a 700-km east-west corridor across upland settings of the Southern Plains. The 117 samples from 39 transects in 13 localities yielded 35,356 shells of land snails. These were recovered from comparable settings across three physiographic provinces that support four distinct biotic districts. The emphasis of this survey was to strengthen the biogeographic database for living terrestrial gastropod populations in the Southern Plains region. Because land snails have rather limited ranges of movement, the species from the 117 samples amount to samples of 39 individual assemblages. For these we have collected comprehensive information on vegetation, slope, aspect, soil, and other edaphic conditions. These findings should be considered a work in progress.

As noted above, earlier collections of land snails are reported from Southern Plains settings (Leonard 1943, Hoff 1962, Branson 1972, Neck 1984, 1990). Unfortunately, at present it is difficult to make meaningful comparisons with findings from most of these earlier collections. The principal problem involves lack of information on the collection methods utilized, on whether snails were living or fresh when collected, and on quantification of assemblages.

The SPGS documented a shifting pattern of land snail taxa along the corridor from east to west (Appendix 2, Table 1). In this distribution, some species dropped out while others were added to assemblages, corresponding to shifts in environmental conditions, indicating their promise as proxy indicators of past settings. The greatest abundance and diversity occurred in the most mesic, easternmost part of the study corridor. The calcareous rock ledges of the Kubic Ranch locality create conditions (high soil pH, lush vegetation, and protection from fire and grazing) favorable to snail propagation, growth, and preservation (e.g., Coney *et al.* 1982). In the study corridor, protected rock ledges consistently yielded the greatest number and diversity recorded for the sampled landforms. These rocky locations typically act as catchments for fine-textured soil, vegetation detritus, and moisture, all of which are key ingredients for supporting and maintaining land snail communities. Because these rocky slopes and ledges are on the higher points in the landscape, they constitute potential sources from which snail species could be dispersed onto lower settings.

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APPENDIX 1
TRANSECT LOCATION AND HABITAT CHARACTERISTICS

Sampling locations for the Southern Plains Gastropod Survey (SPGS). See Sample Localities section of text for further description.

Transect	Longitude	Elev. (m)	Ann. Precip. (cm)	Hillslope Position	Slope (%)	Aspect	Landforms Sampled
Kubic 6	96° 48-49'	360	86	riparian	13	SSW	riparian woodland
Kubik 1	96° 49-50'	351	86	slope	13	S	toe slope
Kubik 2	96° 49-50'	360	86	shoulder	35	S	rock ledge
Kubik 3	96° 49-50'	366	86	summit	1	-	mesa top
Kubik 4	96° 49-50'	360	86	shoulder	34	NNW	rock ledge
Kubik 5	96° 49-50	351	86	slope	8	NNW	toe slope
Tripp 7	97° 25-26'	317	86	slope	0	-	pasture/broad plain
Tripp 8	97° 25-26'	317	86	slope	6	SW	pasture/broad plain
Bluff Creek 36	97° 30-31'	347	76	summit	0	-	pasture/broad plain
Salt Fork 9	97° 34-35'	320	76	summit	2	S	wooded dune
Salt Fork 10	97° 34-35'	320	76	summit	4	SE	dune
McDaniel 11	98° 26-27'	375	69	upland	3	S	pasture/broad plain
Burnham 12	99° 09-10'	607	66	shoulder	34	N	rock ledge
Burnham 13	99° 09-10'	610	66	summit	1	-	mesa top
Burnham 14	99° 09-10'	607	66	shoulder	32	SSE	rock ledge
Big Salt Plains 15	99° 14-15'	482	66	summit	1	-	dune
Burnham 16	99° 10-11'	567	66	slope	4	WNW	toe slope
Burnham 17	99° 10-11'	518	66	slope	3	W	riparian woodland
Barby 18	100° 03-04'	671	53	summit	1	NNW	pasture/broad plain
Laverty 19	100° 03-04'	664	53	alluvium	0	-	pasture/broad plain
Laverty 20	100° 03-04'	664	53	summit	1	ENE	dune
Hitch 21	101° 20-21'	933	45	summit	0	-	mesa top
Hitch 22	101° 20-21'	914	45	shoulder	26	N	toe slope
Hitch 23	101° 21-22'	881	45	floodplain	0	-	riparian woodland
Black Mesa 24	102° 56-57'	1487	38	summit	0	-	mesa top
Black Mesa 25	102° 56-57'	1463	38	shoulder	0	NNE	rock ledge
Black Mesa 26	102° 56-57'	1323	38	slope	6	NNE	toe slope
Black Mesa 35	102° 56-57'	1463	38	shoulder	55	S	rock ledge
N Carrizo Cr. 27	102° 56-57'	1311	38	floodplain	4	S	riparian woodland
Owensby 59	104° 05-06'	2286	38	shoulder	8	SE	rock ledge, toe slope
Owensby 60	104° 05-06'	2240	38	slope	10	SE	pasture/broad plain, riparian woodland
Owensby 61	104° 05-06'	2192	38	slope	3	E	mesa top, rock ledge
C.S. Ranch 28	104° 49-50'	1940	38	summit	1	SSW	mesa top
C.S. Ranch 29	104° 49-50'	1939	38	shoulder	25	N	toe slope
C.S. Ranch 30	104° 49-50'	1920	38	slope	8	NNE	toe slope
Chase 34	104° 55-56'	1951	38	floodplain	0	-	riparian woodland
Chase 31	104° 56-57'	2219	38	shoulder	38	NNE	rock ledge
Chase 32	104° 56-57'	2231	38	summit	0	-	mesa top
Chase 33	104° 56-57'	2182	38	shoulder	45	S	rock ledge

APPENDIX 2
RAW DATA FOR GASTROPOD ASSEMBLAGES

Gastropod assemblages from the Southern Plains Gastropod Survey (SPGS). Key to landforms: D = dunes; MT = mesa tops; PB = pastures, broad plains; RL = rock ledges; RW = riparian woodlands; TS = toe slopes; WD = wooded dunes; sf = sub-fossil; * = one-half sample.

Collection Locality:	Chase												C.S. Ranch									Owensby									Black Mesa														
Transects:	34			33			32			31			30			29			28			59			60			61			27			35			26			25			24		
Samples:	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
		RW			RL			MT			RL			TS			TS			MT		RL	TS	TS	PB	RW	PB	RL	MT	MT		RW			RL			TS			RL			MT	
Taxon																																													
Cionella lubrica	2			3	33	25	1															19	5																						
Gastrocopta armifera	1																																												
Gastrocopta contracta																																													
Gastrocopta cristata																																													
Gastrocopta holzingeri																						19	24	13																					
Gastrocopta pellucida					6	2										12	74	19													31	6	156	85	631	205	7	26	45	192	135	361			
Gastrocopta pentodon																																													
Gastrocopta pilsbryana				67	62	30				2	21	54																																	
Gastrocopta procera																															62	75	246				17	43	37	43	12	12			
Gastrocopta:species uncertain																						21																							
Pupilla muscorum																						16				5		66	7	3				88	39	388				27	31	19			
Pupoides albilabris													31	2	2	2	12		5	3	6										2		15	5	17	10		8	12	3		4	16	27	28
Vallonia gracilicosta	28	3							24													36	31	14		5		18	5	7	140	52	74	67	609	463	63	4		116	423	224			
Vallonia parvula																															2	3	4												
Vallonia sp. [Juveniles]	44	6		1					33													45	28	6		34		23	6	6	302	117	179	44	768	519	94	21		196	834	473			
Helicodiscus nummus																																													
Helicodiscus parallelus																															1	1				1					1	7			
Helicodiscus singleyanus																															1		4						3		2	12	10	10	1
Succineidae									2				3	1	3					1													1	2	9	5	9			5	1				
Euconulus fulvus																						7	2			1		1	5	1															
Euconulus trochulus																																													
Glyphyalinia indentata					2	3																																							
Hawaiia minuscula																	6	4				8	5								8				24	3				13	3	6			
Zonitoides arboreus				3	24		36			6	1	22										3	2																						
Vitrina pellucida																						23		1		18																			
Deroceras laeve																																													
Millerelix dorfueilliana																																													
Millerelix sp. [Juveniles]																																													
Juveniles = Terrestrial Taxa	12			23	24	26	15			1	4	32	3	1	2	12		3	1			68	16	6	1	16		93	17	1	61	59	392	147	195	544	1	47	49	88	62	175	35	39	21
Totals:	**87**	**9**	**0**	**97**	**151**	**86**	**52**	**0**	**59**	**9**	**26**	**108**	**37**	**4**	**7**	**26**	**92**	**26**	**6**	**4**	**6**	**265**	**113**	**40**	**1**	**79**	**0**	**201**	**40**	**18**	**610**	**313**	**1071**	**438**	**2292**	**2138**	**191**	**149**	**146**	**683**	**1504**	**1293**	**61**	**76**	**50**
Aquatic Snails																															1	1													
Number of Taxa:	**3**	**1**	**0**	**3**	**5**	**4**	**2**	**0**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**2**	**1**	**2**	**1**	**8**	**6**	**3**	**0**	**4**	**0**	**3**	**3**	**3**	**8**	**5**	**7**	**5**	**6**	**7**	**4**	**4**	**4**	**7**	**8**	**8**	**2**	**2**	**2**

APPENDIX 2 (continued)

Collection locality:	Hitch									Laverty						Barby			Burnham						Big Salt Plain			Burnham								
Transects:	23			22			21			20			19			18			17			16			15			14			13			12		
Samples:	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A*	B*	C
Landform Niches:	RW			TS			MT			D			PB			PB			RW			TS			D			RL			MT			RL		
Taxon																																				
Cionella lubrica																																				
Gastrocopta armifera																																				
Gastrocopta contracta																																				
Gastrocopta cristata	331	159	92							1			16	2	49											2										
Gastrocopta holzingeri																																				
Gastrocopta pellucida	1s.f.																		31	134	16			2	55	7		543	134	1279	83	88	15	210	136	273
Gastrocopta pentodon	1s.f.												1s.f.																							
Gastrocopta pilsbryana																																				
Gastrocopta procera	53	1	5	239	190	14		6	15				1			215	69	227	4	17	1	441	51	10	5	6	3	180	123	174	83	130	86	74	136	210
Gastrocopta: species uncertain																																				
Pupilla muscorum																																				
Pupoides albilabris	20	7	4	27	40	8	11	3	5	1	4	4	4		10	17	9	24		2	1	3	1		1	1	1	6	4	9	2	3	4	5	5	1
Vallonia gracilicosta																				1s.f.																
Vallonia parvula	24	60	4																															271	91	86
Vallonia sp.	31	91	11																															507	199	166
Helicodiscus nummus																				6		13	1					30	16	28	6	11	3	10	21	13
Helicodiscus parallelus	38																		1	3		1	1					5	6	6	1			9	1	1
Helicodiscus singleyanus	10	2	6													1	9	2		3								10	8					2	9	
Succineidae	14	1	1	184	40		101	1	2		1	2	1	1		17	4	10		1																
Euconulus fulvus																																				
Euconulus trochulus																																				
Glyphyalinia indentata																																				
Hawaiia minuscula	100	16	8	109		3	2	3					1				2		1			1	2					15	22	16	2			10	46	20
Zonitoides arboreus																																				
Vitrina pellucida																																				
Deroceras laeve		1	2																										1					1	2	
Millerelix dorfueilliana																																				
Millerelix sp.																																				
Juveniles = Terrestrial Taxa	221	93	34	244	185	17	23	5	9	1		10	17		11	103	29	141	22	95	4	382	88	16	28	5	4	363	292	804	47	212	31	247	409	263
Totals:	**844**	**431**	**167**	**803**	**455**	**42**	**137**	**18**	**31**	**3**	**5**	**16**	**41**	**3**	**70**	**353**	**122**	**404**	**59**	**262**	**22**	**841**	**144**	**28**	**89**	**21**	**8**	**1152**	**606**	**2316**	**224**	**444**	**139**	**1346**	**1055**	**1033**
Aquatic Snails			1																																	
Number of Taxa:	**8**	**8**	**8**	**4**	**3**	**3**	**3**	**3**	**3**	**2**	**2**	**2**	**5**	**2**	**2**	**4**	**5**	**4**	**4**	**7**	**3**	**5**	**5**	**2**	**3**	**4**	**2**	**7**	**8**	**6**	**6**	**4**	**4**	**9**	**9**	**7**

APPENDIX 2 (continued)

Collection locality:	**McDaniel**			**Salt Fork**						**Bluff Creek**			**Tripp**						**Kubic Ranch**																	
Transects:	11			10			9			36			8			7			6			5			4			3			2			1		
Samples:	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A*	B	C*	A	B	C	A*	B*	C*	A	B	C
Landform Niches:	PB			D			WD			PB			PB			PB			RW			TS			RL			MT			RL			TS		
Taxon																																				
Cionella lubrica																																				
Gastrocopta armifera							4	2														1	8	3	25	20	34				8	16	2	7	1	5
Gastrocopta contracta																			4	23	24		6	3	87	32	112				121	15	28	17	31	8
Gastrocopta cristata																																				
Gastrocopta holzingeri																					38											14				
Gastrocopta pellucida				5	1		107	116	83													2	2	1	48	25	114				219	63	194			1
Gastrocopta pentodon																			3	13	22															
Gastrocopta pilsbryana																																				
Gastrocopta procera	10	6	10	3		1	4	2		81	27			5	5			1		2		34	86	111	156	91	337	2	1	35	78	98	101	96	113	85
Gastrocopta species uncertain																																				
Pupilla muscorum																																				
Pupoides albilabris					1		1			16	5									1		2	7	4	4	4	14		6	5	15	13	8	12	12	24
Vallonia gracilicosta																																				
Vallonia parvula				2		2	146	285	131												20	3	14	12		2	15				112	144	41			
Vallonia sp.							273	479	176												47	13	23	27	1	5	18				172	250	145			
Helicodiscus nummus																					2		1		9	23	13				4	32	21			
Helicodiscus parallelus										1											3				64	58	66				32	19	28			
Helicodiscus singleyanus		1								8															1	14	21				15	5	17			
Succineidae																		2														2		36	22	2
Euconulus fulvus																																				
Euconulus trochulus																					18															
Glyphyalinia indentata																				10	24	1	11	1	6	5	10	1			17	12	8	14	10	10
Hawaiia minuscula						2					2			1					3	1	37		4		55	31	68				26	21	19		12	4
Zonitoides arboreus																																				
Vitrina pellucida																																				
Deroceras laeve														1						1	9		2				1									1
Millerelix dorfueilliana																				1	1				7	11	1				9	5	2			
Millerelix sp.																				1	3				21	9	10				37	19	28			
Juveniles = Terrestrial Taxa	2	5	3	3	1	2	38	24	22	41	24			1	3				5	22	71	17	56	35	143	82	291	1	7	28	186	87	234	86	158	122
Totals:	**12**	**12**	**13**	**13**	**3**	**7**	**573**	**908**	**412**	**147**	**58**	**0**	**0**	**8**	**8**	**0**	**0**	**3**	**15**	**75**	**319**	**73**	**220**	**197**	**627**	**412**	**1125**	**4**	**14**	**68**	**1051**	**815**	**876**	**268**	**359**	**262**
Aquatic Snails																																				
Number of Taxa:	**1**	**2**	**1**	**3**	**2**	**3**	**5**	**4**	**2**	**4**	**3**	**0**	**0**	**3**	**1**	**0**	**0**	**2**	**3**	**8**	**12**	**6**	**10**	**9**	**11**	**12**	**13**	**2**	**2**	**2**	**12**	**14**	**12**	**6**	**7**	**9**

Terrestrial gastropod fauna of Northeastern Wisconsin and the Southern Upper Peninsula of Michigan

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Abstract: The terrestrial gastropod fauna of eastern Wisconsin and the southern Upper Peninsula of Michigan is among the most poorly known in the eastern United States. To document this fauna, 242 sites were analyzed across 22 counties and 20 habitat types. A total of 82 taxa were encountered, or approximately half of those reported from the western Great Lakes region. Some of these are limited in the eastern USA to no more than 50 counties, including *Catinella exile, Catinella* cf. *gelida, Hendersonia occulta, Planogyra asteriscus, Strobilops affinis, Vallonia gracilicosta, Vertigo bollesiana, Vertigo cristata, Vertigo hubrichti, Vertigo modesta, Vertigo morsei, Vertigo nylanderi, Vertigo paradoxa,* and *Zoogenetes harpa*. Thirty-one taxa demonstrated significant variation in occurrence frequency across the landscape. Fourteen increased in frequency towards the southwest, another thirteen increased in frequency towards the northeast, two had their highest occurrence frequencies on the Door and Garden Peninsulas, and two taxa had their lowest occurrence frequencies on the Door and Garden Peninsulas. Fully 50% of the fauna also demonstrated significant differences in their occurrence frequencies between five broadly-defined habitat groupings (rock outcrops, upland forests, lowland forests, upland grasslands, and lowland grasslands). Fifteen taxa favored lowlands (either forest or grassland), thirteen favored rock outcrops, and nine favored both rock outcrop and upland forest sites. Because of these geographic and ecological trends, conservation of this fauna will likely require protection of a number of different habitats (particularly carbonate cliff, rocky forest, lowland forest, and fen sites) spread across the study area.

Key words: biodiversity, biogeography, Niagaran Escarpment, Midwestern U.S.A.

Thorough investigations into terrestrial gastropod biodiversity in the upper Midwest have been largely limited to Michigan (*e.g.*, Walker 1906, Burch and Jung 1988, Hubricht 1985, Pearce *et al.* 1992), the Paleozoic Plateau of northeastern Iowa, northwestern Illinois, southeastern Minnesota and southwestern Wisconsin (Frest 1981, 1982, 1987, 1990, 1991, Theler 1997), the Loess Hills of western Iowa (Frest and Dickson 1986), and the Black Hills of South Dakota and Wyoming (Frest and Johannes 1993). These regions have generally been found to support a diverse fauna including a number of rare taxa such as *Catinella* cf. *gelida* (F. C. Baker, 1927); *Discus macclintocki* F. C. Baker, 1928; *Hendersonia occulta* (Say, 1831); *Vertigo arthuri* von Martens, 1882, *Vertigo hubrichti* (Pilsbry, 1934); *Vertigo meramecensis* Van Devender, 1979; *Vertigo morsei* Sterki, 1894; and *Vertigo paradoxa* Sterki, 1900.

However, over most of the region the modern land snail fauna is poorly known. In the six counties bordering Lakes Michigan and Huron in the Upper Peninsula of Michigan, only 62 species and 145 county occurrence records had been previously reported (Hubricht 1985). Prior investigations of modern northeastern Wisconsin land snails (Levi and Levi 1950, Solem 1952, Teskey 1954, Hubricht 1985) identified only 42 taxa and 122 county occurrence records across a 20-county region.

This paper summarizes findings of a land snail survey conducted from 1996-2001 in eastern Wisconsin and the southern Upper Peninsula of Michigan along the northern and western shores of Lakes Michigan and Huron, a region that straddles the boundary of the Northern and Interior Molluscan Provinces (Burch 1962), and harbors many unique natural habitats with uncommon plant species (Curtis 1959). Individual sites in this area are known to support land snail communities containing up to 34 taxa per 1000 m^2 (Nekola 1999). The data collected in this survey will be used to help better document: (1) the composition of the regional land snail fauna; (2) the geographic distribution of taxa within the region; and (3) the general habitat preferences of taxa.

MATERIALS AND METHODS

Study Area

This study was centered on 22 counties along the northern and western shores of Lakes Michigan and Huron (Fig. 1). Samples were collected from Chippewa, Delta, Luce, Mackinac, and Schoolcraft counties in Michigan and from Brown, Calumet, Dodge, Door, Fond du Lac, Green Lake, Kewaunee, Langlade, Manitowoc, Marinette, Oconto, Outagamie, Ozaukee, Sheboygan, Shawano, Washington, and Waushara counties in Wisconsin. Important geographic landmarks in this area that can be used to help describe species ranges include: Lake Winnebago, a large lake found south of Green Bay; the Door Peninsula, which separates

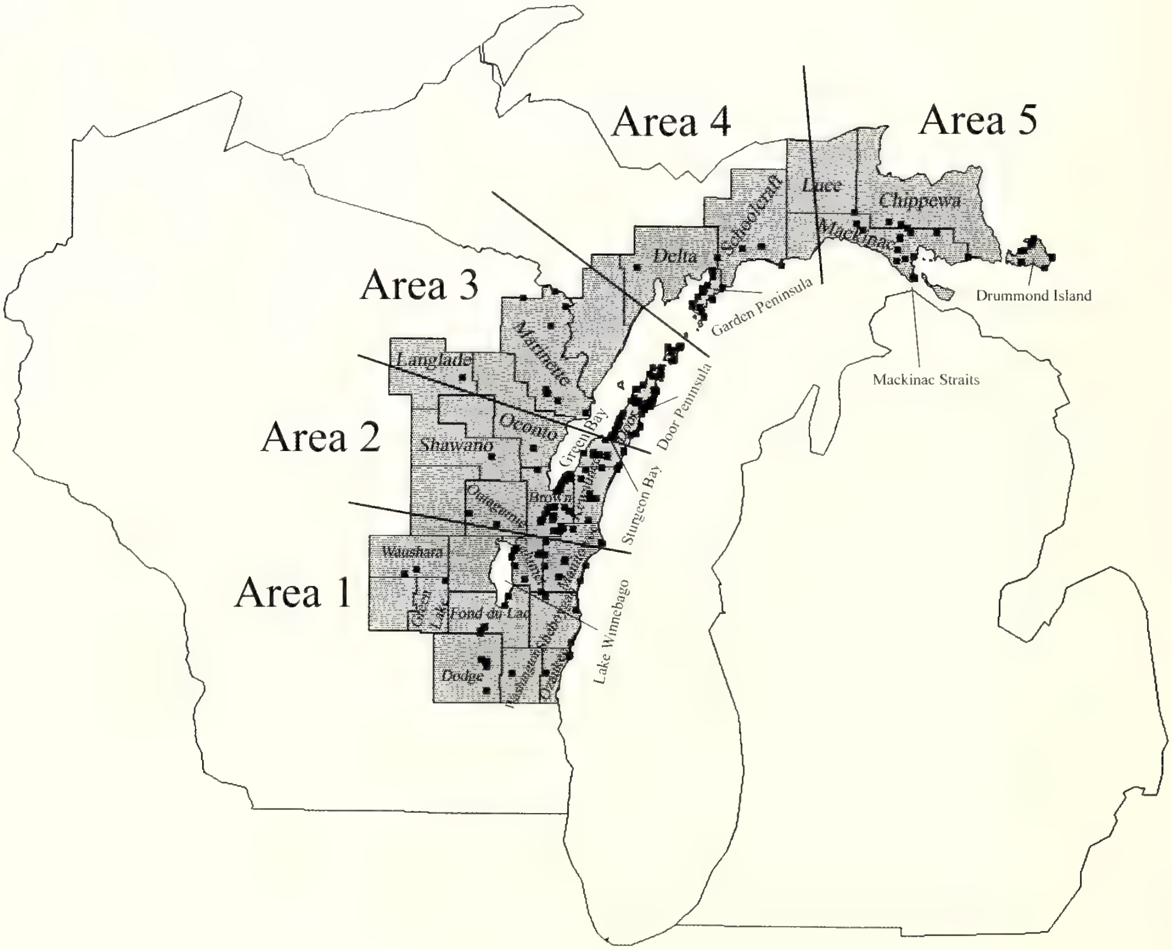
Area 4
Area 5
Luce
Chippewa
Schoolcraft
Mackinac
Delta
Drummond Island
Garden Peninsula
Area 3
Marinette
Langlade
Oconto
Shawano
Mackinac Straits
Area 2
Green Bay
Door
Door Peninsula
Kewaunee
Brown
Outagamie
Manitowoc
Sturgeon Bay
Calumet
Waushara
Area 1
Green Lake
Fond du Lac
Sheboygan
Lake Winnebago
Dodge
Washington
Ozaukee

Figure 1. Map of the study area, showing outline of the states of Michigan and Wisconsin, and counties included in study region. Grey shading represents maximum extent of collected samples. Black squares represent the location of all 242 sample sites. Dark lines demarcate the five biogeographic areas used for statistical analysis of geographic trends in species occurrence frequency. Names and locations of the major geographic landmarks mentioned in text are also provided.

Lake Michigan from Green Bay in northeastern Wisconsin; Sturgeon Bay, which almost bisects the center of the Door Peninsula; the Garden Peninsula, which separates Lake Michigan from Big Bay de Noc in the Upper Peninsula; the Straits of Mackinac, which join Lakes Michigan and Huron in the eastern Upper Peninsula; and Drummond Island, which is the eastern-most extension of the Upper Peninsula.

The bulk of this region is underlain by calcareous bedrock and tills associated with the Niagaran Escarpment, a band of outcropping Silurian limestones and dolomites that extend from western New York state to northeastern Iowa. In eastern Wisconsin the Niagaran Escarpment extends from Dodge County up the eastern shore of Lake Winnebago and the western side of the Door Peninsula to Rock Island. In the Upper Peninsula, the Niagaran Escarpment extends from the Garden Peninsula eastward through the Mackinac Straits to Drummond Island. Individual outcrop areas are isolated from one another in the region by glacial or lacustrine sediments, and are more widely spaced (up to 90 km) in Michigan.

The climate of this region is characterized by mean maximum summer temperatures ranging from 30°C in the southwest to 23°C in the northeast. Mean minimum January temperatures range from –5°C along the lakeshore in the south to –13°C in the north. Annual precipitation ranges from 710 mm in the Door Peninsula to 810 mm in the eastern Upper Peninsula. In proximity to the Great Lakes shore the climate is buffered, being warmer in the winter, cooler in the summer, and having a longer growing season as compared to inland areas of similar latitude (Eichenlaub *et al.* 1990).

Table 1. Habitat types sampled per county. The three sampled Rock Outcrop habitat types are Carbonate Cliff (RO1), Lakeshore Carbonate Ledge (RO2), and Igneous Cliff (RO3). The five sampled Upland Forest habitat types are Oak-Hickory (UF1), Maple-Basswood (UF2), Hemlock-Yellow Birch (UF3), Lakeshore (UF4), and Rocky (UF5). The five sampled Lowland Forest habitats types are Floodplain (LF1), Black Ash (LF2), Tamarack (LF3), White Cedar (LF4), and Shrub Carr (LF5). The three sampled Upland Grassland habitat types are Sand Dune (UG1), Alvar (UG2), and Old Field (UG3). The four sampled Lowland Grassland habitat types are Sedge Meadow (LG1), Fen (LG2), Calcareous Meadow (LG3), and Cobble Beach (LG4).

State/County	Habitat Code																				
	RO1	RO2	RO3	UF1	UF2	UF3	UF4	UF5	LF1	LF2	LF3	LF4	LF5	UG1	UG2	UG3	LG1	LG2	LG3	LG4	Total
Michigan																					
Chippewa	9	1						2			2				1		1			2	18
Delta	6	1					1	2			1				3				2	1	17
Luce								1													1
Mackinac	1							3				4					1	2			11
Schoolcraft	1	1						2			1									1	6
Wisconsin																					
Brown	14			1		1		3		1	2	2			2			1	1		28
Calumet	5			1				1			2						1				10
Dodge	5																				5
Door	30	19			1		5	6		1	4		1					4	1	2	74
Fond du Lac	7																				7
Green Lake																		1			1
Kewaunee		1					1	1			4	2	1				1	1	1		13
Langlade								1													1
Manitowoc	2				1		5	1	2	3	5			1		1		1	1		23
Marinette			2							1	2	2						1	3		11
Oconto											1										1
Outagamie	1											1									2
Ozaukee							1	1			1					1		1			5
Shawano	1																				1
Sheboygan							2				1					1					4
Washington																		1			1
Waushara											1							1			2
Total	82	23	2	2	2	1	15	24	2	6	27	11	2	1	6	3	4	14	9	6	242

During the late Pleistocene the entire area was covered by continental glaciers. Rapid retreat of this ice sheet, and partial removal of till by meltwaters, began 15,000 B.P. (Maher and Mickelson 1996). This period was followed by approximately 2000 years of severe cold that led to further till removal through periglacial erosion (Steiglitz *et al.* 1980). These processes have allowed for a more frequent exposure of bedrock in the study region as compared to surrounding landscapes.

Study Sites

A total of 242 sites were surveyed for terrestrial gastropods (Fig. 1; Table 1). The number of samples per county ranged from 74 (Door) to 1 (Green Lake, Langlade, Luce, Oconto, Shawano, and Washington). Sites were selected if they represented typical examples of their respective habitat, and (except for anthropogenic habitats) were undisturbed. Most surveyed sites were within 60 km of the shore.

Collections were made from 20 habitat types known or suspected to support diverse and/or interesting land snail communities (Nekola 1999: Table 1). These habitats can be broadly grouped into five categories: rock outcrops, upland forests, lowland forests, upland grasslands, and lowland grasslands.

Three types of rock outcrop sites were surveyed. Carbonate cliffs (82 sites) are 3-20 m tall, wooded limestone or dolomite outcrops that typically support moss, fern, and soil-covered ledges. Lakeshore carbonate ledges (23 sites) are <3 m tall, wooded limestone or dolomite outcrops that are within 4 km of the Lake Michigan or Lake Huron shore. Sampling of igneous cliffs in the region was restricted (2 sites) to 2-8 m tall ultramafic Precambrian outcrops located along the Menominee River on the Wisconsin-Michigan border in Marinette County, one of the few places in the study region where igneous rocks are exposed.

Five types of upland forest habitats were surveyed. Three of these had deep, non-rocky soils, and were characterized by their canopy composition, including oak-hickory (2 sites), maple-basswood (2 sites), and hemlock-yellow birch (1 site) forests. Lakeshore forests (15 sites) were found on steep slopes of unconsolidated lacustrine material adjacent to the Great Lakes shoreline. Rocky woodlands (24 sites) were upland tracts with rocky soils derived from either local bedrock or glacial till.

Five types of lowland forests were surveyed. Floodplain forests (2 sites) occur on silty or sandy soils adjacent to streams. Black ash (6 sites), tamarack (27 sites), and white cedar (11 sites) forests were typically found in areas underlain by calcareous bedrock or till. While surficial soil chemistry on these sites can vary from acidic (where *Sphagnum* moss is abundant) to neutral or alkaline (where *Sphagnum* is largely absent), litter collection was generally limited to the latter microsites. Shrub-carr habitats (wetland areas dominated by shrub thickets, see Curtis, 1959; 2 sites) had a canopy of alder, willow, and dogwood, with a ground layer consisting primarily of sedges.

Only three types of upland grasslands were surveyed, as the regional climate generally favors development of forest communities in most upland situations. Sand dunes (1 site) are xeric grasslands found along the Great Lakes shore. Alvars (6 sites) are treeless areas developed on flat expanses of carbonate bedrock that are covered by little (or no) soil. While such sites are typically xeric by mid-summer, shallow pools are common in the spring. Old fields (3 sites) are early successional grasslands that have developed following agricultural abandonment.

Four types of lowland grassland habitats were surveyed. Sedge meadows (4 sites) are composed of a variety of wetland sedge and grass species, and often support scattered clumps of willows and dogwood. Fens (14 sites) are peatland areas found at sites of ground water discharge. They maintain higher soil moisture and cooler soil temperatures than are otherwise found in the surrounding landscape (Nekola 1994). Sampling was conducted only from sites in which *Sphagnum* was either uncommon or lacking. Calcareous meadows (9 sites) are often sparsely vegetated wetlands found on mineral (rather than organic) soils. Cobble beaches (6 sites) are constantly wet grasslands developed on limestone or dolomite pavement along the Great Lakes shore. Little or no soil development exists on these sites except along bedrock fractures.

Field Methods

Documentation of terrestrial gastropods from each site was accomplished by hand collection of larger shells and litter sampling for smaller taxa from representative 100-1000 m≤ areas. Soil litter sampling was primary used as it provides the most complete assessment of site faunas (Oggier *et al.* 1998). As suggested by Emberton *et al.* (1996), collections were made at places of high micro-mollusc density, with a constant volume of soil litter (approximately 4 l) being gathered from each site. For woodland sites, sampling was concentrated: (1) along the bases of rocks or trees; (2) on soil-covered bedrock ledges; and/or (3) at other places found to have an abundance of shells. For grassland sites, samples consisted of: (1) small blocks (ca. 125 cm^3) of turf; (2) loose soil and organic litter accumulations under or adjacent to shrubs, cobbles, boulders, and/or hummocks; and (3) other locations observed to have an abundance of shells.

Laboratory Procedures

The location of each sample was marked on USGS 7.5′ topographic maps. The latitude-longitude coordinates for each was then determined through digitization of these maps using the ATLAS DRAW software package.

Samples were slowly and completely dried in either a low-temperature soil oven (ca. 80-95°C) or in full sun in a greenhouse. Dried samples were then soaked in water for 3-24 h, and subjected to careful but vigorous water disaggregation through a standard sieve series (ASTME 3/8" [9.5 mm], 10 [2.0 mm], 20 [0.85], and 40 [0.425 mm] mesh screens). Sieved sample fractions were then dried and passed again through the same sieve series. These dry, resorted fractions were hand-picked against a neutral-brown background. All shells and shell fragments were removed.

All recovered, identifiable shells from each site were assigned to species (or subspecies) using the author's reference collection and the Hubricht Collection at the Field Museum of Natural History (FMNH). Some additional specimens representing Holarctic taxa were verified by Robert Cameron of the University of Sheffield. All specimens have been catalogued and are housed in the author's collection at the University of Wisconsin - Green Bay. Nomenclature generally follows that of Turgeon *et al.* (1998). Where these differ from Hubricht (1985), the latter has been provided in brackets. The few exceptions to this are detailed more fully below in the annotated list under the entry for that taxon.

Given the diversity in the region within the genera *Vertigo* and *Gastrocopta*, and the few published images of these taxa, a plate of SEM micrographs representing a selection of these taxa has been provided to aid in their future identification (Fig. 2). These images are based on representative specimens from the UWGB collection that were located in or adjacent to the study region, and hence do not represent paratypes or topotypes. Micrographs were taken with a Hitachi S-2460N Scanning Electron Microscope in N-SEM Mode (10 Pa; 22 kV) with a backscatter detector and #2 Gamma Correction.

Statistical Tests

Contingency table analyses were used to assess which taxa differed in their occurrence frequencies between five similar-sized biogeographic areas within the region (Fig. 1). Area 1 (51 sites) ranged south of Lake Winnebago. Area 2 (64 sites) ranged from Sturgeon Bay and central Oconto County to the north side of Lake Winnebago. Area 3 (74 sites) ranged from Rock Island and Marinette County to Sturgeon Bay and central Oconto County. Area 4 (23 sites) ranged across Delta and Schoolcraft counties, including all of the Garden Peninsula. Area 5 (30 sites) ranged from Drummond Island west to central Mackinac counties.

Table 2. Number of sites at which taxon occurred in each county; an "x" represents species reported by Hubricht (1985) from a given county, but which were not observed in that county during this study.

Taxon	State and County																						
	Michigan					Wisconsin																	
	Chippewa	Delta	Luce	Mackinac	Schoolcraft	Brown	Calumet	Dodge	Door	Fond du Lac	Green Lake	Kewaunee	Langlade	Manitowoc	Marinette	Oconto	Outagamie	Ozaukee	Shawano	Sheboygan	Washington	Waushara	Total
Allogonia profunda		1			x	4	4	3	8	6		x		1	x	x	x	x	x				27
Anguispira alternata	11	11	1	4	2	16	7	4	50	7		2	x	5	2	x	1	2	1	1			128
Carychium exiguum	4	3		5	2	8	4		16		1	10		5	7	1	1	2		1	1	2	73
Carychium exile	4	8		3	4	19	6	5	28	7		7		8	4			2	1				107
Catinella avara	1	2	x	x	1	3	3		3			3		2	x		x			1			19
Catinella exile	1	1		1					2		1										1	1	8
Catinella cf. *gelida*						4	4	5		5									1				19
Catinella cf. *vermeta*	1																						1
Cochlicopa lubrica	3	2	1	3	2	17	5	2	13	3		4		8				3	x	3		1	70
Cochlicopa lubricella		2		2	1	11	2	2	7	1		3		2	3		1					1	38
Cochlicopa morseana	5	4	1	1			1		5			2	1				1		1				22
Columella simplex	14	12	1	7	4	8	2	1	56	2		5		9	4		2		1	1		1	129
Deroceras spp.	2	5		1	1	12	6	5	7	7	1	5	1	5	5		1	1			1	1	67
Discus catskillensis	13	11	1	6	4	11	5	5	54	7		4	1	5	4	x	1		1				133
Discus whitneyi	3	1		1	2	7	3		3	1	1	4	1	3	1			1		1	1		34
Discus patulus						x																	
Euchemotrema fraternum	5	3	1	3	1	4	5	4	22	6		x	x		x	x			1				55
Euchemotrema leai	1	1		x	1	4	2		5		1	5		2	2	1					1	2	28
Euconulus alderi	2	2		4	2	3	3		7		1	7		2	4	1		1		1	1	2	43
Euconulus fulvus	11	8	1	3	3	11	3	3	40	5			1	11	4		2	1					107
Euconulus polygyratus	5	4	1	4	2	6	3	1	24	1		2		2									55
Gastrocopta armifera						6		3	2	2				1			1						15
Gastrocopta contracta	4	6	1	1		18	7	5	30	7	1	4		7	2		2	1	1		1	1	99
Gastrocopta corticaria						8	5	5	6	7													31
Gastrocopta holzingeri		2				15	6	5	8	7		1		4		1	1		1				51
Gastrocopta pentodon	4	8			2	16	5	3	38	6		2		6	2		2		1				95
Gastrocopta similis								1															1
Gastrocopta tappaniana	5	4		4	1	9	4		11		1	9		7	2	1	2	2		2	1	2	67
Glyphyalinia indentata	7	7	1	3	x	11	2	2	23			2		1	1	1	1		1				63
Glyphyalinia rhoadsi	3	2	1	1	x	1			5										1				14
Glyphyalinia wheatleyi	x	x		1					1														2
Guppya sterkii		1				2			1														4
Haplotrema concavum	1					1								3									5
Hawaiia minuscula	3	4			1	18	7	5	8	7	1	2		3	2	1	2	1	1		1	2	69
Helicodiscus parallelus	8	4	1	4	1	9	5	2	4	2	1	5		5	3	1	2	1			1	1	60
Helicodiscus shimeki	6	10	1	5	3	16	8	4	53	7		5		7	2		1	1	1				130
Hendersonia occulta		x				15	1		20			2		9				1		2			50
Mesodon thyroidus						x			4						x	x			x				4
Neohelix albolabris	1	x	x	x	x				9	x			x	x		x		1	x				11
Nesovitrea binneyana	10	6	1	7	x	3	2		15	1			1	2	2								50
Nesovitrea electrina	3	5	x	3	2	8	3		18		1	10		6	7	1		2		2	1	2	74
Novisuccinea ovalis		1		x		13	5	1	20	6		5		2	1	x		2		1	1		58
Planogyra asteriscus	1	1		4	2										1					x			9
Pomatiopsis lapidaria						1						x		2	1								4
Punctum minutissimum	17	14	1	7	6	9			64			6		1	5		1		1	1			133
Punctum n.sp.							2		1		1				2						1	1	9
Punctum vitreum						12	6	5	1	7		2		13			1	1		1			49
Pupilla muscorum				2																			2
Pupoides albilabris						1																	1
Stenotrema barbatum														x				2			1		3
Striatura exigua	10	4	1	10	2	4			21	x		8		2	6	1						1	70
Striatura ferrea	6	4	1	6	1	2			14			2		2	2	1							41
Striatura milium	13	12	1	8	5	7	2		44	1		10		8	9	1	1	2				1	125
Strobilops aenea									1														1
Strobilops affinis				1		4	1		1		1	4		2	2		x				1	2	19
Strobilops labyrinthica	14	14	1	9	4	20	6	5	62	7		9		9	10	1	1	2	1			1	176
Vallonia costata	x	2	x	x	2	12	2	1	7	1		2		6	3			1		1		1	41
Vallonia excentrica						1												1		1			3
Vallonia gracilicosta	5	3				7	1	1	12	3													32
Vallonia perspectiva							5	1		6													12
Vallonia pulchella	x	2		x	x	9		1	2	1		2		5	4	1		1	x	1			29
Vertigo bollesiana	3	5				8	3		45			2	1	2	1		2		1				73
Vertigo cristata	4	2		3	1				12						3								25
Vertigo elatior	5	5		4	2	4	1		11		1	5		7	5	1	1	2	x	1	1	2	58
Vertigo gouldi	10	9	1	4	3	15	8	5	48	7		2		6	2		2		1				123
Vertigo hubrichti	5	8			3	8		1	41	6				1									73
Vertigo milium						13	3	3	5	1	1	2		3	1	1	2	2	x		1	2	40
Vertigo modesta													1										1
Vertigo morsei	x			2					3													1	6
Vertigo nylanderi	2	1		1	1	3	2		2			2		1		1						1	17
Vertigo ovata	1	1			1	1	2		5		1	2		2	5	1	x			1			23
Vertigo paradoxa	7	1		1	3				4						2								18
Vertigo pygmaea	1					16	1	1	2	1		2		5	2	1		1		2			35
Vertigo tridentata						1		2		2													5
Vitrina limpida	3	2	1	4	2				2			1		1						1			17
Webbhelix multilineata						1	4		1						x	x			x				6
Zonitoides arboreus	16	9	1	7	4	18	8	5	59	7		9	1	12	9	1	2	2	1		1	1	173
Zonitoides limatulus									x														
Zonitoides nitidus	1	1		x		7	3		6			1		5				1		3		1	29
Zoogenetes harpa	4	3		2	1				1														11
Total richness	55	57	28	50	46	63	51	36	70	38	17	49	12	53	47	29	31	30	27	22	19	27	84

Table 3. Number of taxon occurrences per habitat type. The three sampled Rock Outcrop habitat types are Carbonate Cliff (RO1), Lakeshore Carbonate Ledge (RO2), and Igneous Cliff (RO3). The five sampled Upland Forest habitat types are Oak-Hickory (UF1), Maple-Basswood (UF2), Hemlock-Yellow Birch (UF3), Lakeshore (UF4), and Rocky (UF5). The five sampled Lowland Forest habitats types are Floodplain (LF1), Black Ash (LF2), Tamarack (LF3), White Cedar (LF4), and Shrub Carr (LF5). The three sampled Upland Grassland habitat types are Sand Dune (UG1), Alvar (UG2), and Old Field (UG3). The four sampled Lowland Grassland habitat types are Sedge Meadow (LG1), Fen (LG2), Calcareous Meadow (LG3), and Cobble Beach (LG4).

Taxon	Habitat Code																				
	RO1	RO2	RO3	UF1	UF2	UF3	UF4	UF5	LF1	LF2	LF3	LF4	LF5	UG1	UG2	UG3	LG1	LG2	LG3	LG4	Total
Allogona profunda	19	3						5													27
Anguispira alternata	79	18	2	1	1		8	15			1	2								1	128
Carychium exiguum	4					1		2		4	24	10	2		1		3	13	5	4	73
Carychium exile	52	11	1			1	8	10	1	4	3	6			3	2		2	3		107
Catinella avara	1										6				4		1	1	3	3	19
Catinella exile																		5		3	8
Catinella cf. *gelida*	19																				19
Catinella cf. *vermeta*															1						1
Cochlicopa lubrica	25	3		2			9	15			3	3			2	2	2	2	1	1	70
Cochlicopa lubricella	17	2		1			1	8		1		1			1		1	2	3		38
Cochlicopa morseana	9	2					2	6			1	1							1		22
Columella simplex	53	21	1		1	1	12	13		2	5	6	1		2		2	3	2	5	130
Deroceras spp.	34	1	1	1			1	3	1	3	6	2						8	4	2	67
Discus catskillensis	73	21	2		1		5	16		2	3	4	1			1	1		2	1	133
Discus whitneyi	8	2					1	6		1	5	3				1	2	2	1	2	34
Euchemotrema fraternum	42	7						5				1									55
Euchemotrema leai	1							1			6	2	2		1		2	7	3	3	28
Euconulus alderi								1		3	17	3	1				2	11	3	2	43
Euconulus fulvus	48	17	2		1	1	6	12	1	3	2	4		1	1			3	4	1	107
Euconulus polygyratus	24	9			1	1	3	11		1		2				1		1	1		55
Gastrocopta armifera	13						1								1						15
Gastrocopta contracta	57	8				1	1	6		3	6	3			1			6	6	1	99
Gastrocopta corticaria	30	1																			31
Gastrocopta holzingeri	42	2				1	1	1		1	1			1	1						51
Gastrocopta pentodon	61	8			1	1	1	5		5	6	2			2	1			1	1	95
Gastrocopta similis	1																				1
Gastrocopta tappaniana	3						2	3		3	21	4	1		5		3	12	6	4	67
Glyphyalinia indentata	34	7			1		1	8		1	2	2			2	1		1	2	1	63
Glyphyalinia rhoadsi	8	1					1	4													14
Glyphyalinia wheatleyi		1						1													2
Guppya sterkii	3							1													4
Haplotrema concavum	1					1				2	1										5
Hawaiia minuscula	38	1					2	5		1	5	3			1			4	5	4	69
Helicodiscus parallelus	21	4						11		1	12	4			2			4	2		60
Helicodiscus shimeki	66	19	1	1	1	1	7	14		3	4	6			2			2	2	1	130
Hendersonia occulta	28	3				1	8	4	2	1	1	1						1			50
Mesodon thyroidus	3	1																			4
Neohelix albolabris	3	3			1		1	3													11
Nesovitrea binneyana	24	9	1				2	4				5			1	1		1	1	1	50
Nesovitrea electrina	5	3				1	1	1		4	25	7	2		3	1	2	13	4	2	74
Novisuccinea ovalis	26	5		1			8	7			2	2	1			1	1	1	3		58
Oxychilus cellarius								1													1
Oxychilus draparnaudi		1																			1
Oxyloma retusa	1								1	1	2	2			1		2	7	5	4	26
Paravitrea multidentata	44	12			1		1	10													68
Planogyra asteriscus		2	1				1	1				3						1			9
Pomatiopsis lapidaria									1			1						1	1		4
Punctum minutissimum	51	22	1		1	1	8	16		2	9	5	1		4		1	3	4	4	133
Punctum n.sp.											3							5	1		9
Punctum vitreum	28	1					5	4	2	3	3	2						1			49
Pupilla muscorum								1				1									2
Pupoides albilabris																			1		1
Stenotrema barbatum											1							2			3
Striatura exigua	14	8			1	1	3	8		3	15	9	1				1	4	2		70

Table 3. (continued)

Taxon	Habitat Code																				
	RO1	RO2	RO3	UF1	UF2	UF3	UF4	UF5	LF1	LF2	LF3	LF4	LF5	UG1	UG2	UG3	LG1	LG2	LG3	LG4	Total
Striatura ferrea	11	7				1	2	7		3	2	6	1					1			41
Striatura milium	31	20	1		1	1	7	13		5	22	10	2		1		1	6	4		125
Strobilops aenea	1																				1
Strobilops affinis										2	5	2			1		1	5	3		19
Strobilops labyrinthica	76	22	2		1	1	8	13		5	17	9	1	1	3	1	1	7	4	4	176
Vallonia costata	18	2					1	4		1	1	2			1	3	1	2	4	1	41
Vallonia excentrica								1								2					3
Vallonia gracilicosta	31	1																			32
Vallonia perspectiva	11							1													12
Vallonia pulchella	8							4		1	2				1	2	1	3	7		29
Vertigo bollesiana	41	18	1				4	4		2	1	2									73
Vertigo cristata	9	10	2					2			1	1									25
Vertigo elatior					1		1	1		4	20	4	1		2		1	12	6	5	58
Vertigo gouldi	81	20	2	1		1	2	10	1	2	1	2									123
Vertigo hubrichti	54	15					1	2							1						73
Vertigo milium	19							2		2	6	3				1		4	3		40
Vertigo modesta								1													1
Vertigo morsei																		6			6
Vertigo nylanderi						1		1		2	11	2									17
Vertigo ovata										1	4	1					1	4	7	5	23
Vertigo paradoxa	10	3	2					2			1										18
Vertigo pygmaea	15			1			2	3			1				1	2	2	2	6		35
Vertigo tridentata	5																				5
Vitrina limpida	4						2	5				1			2	2				1	17
Webbhelix multilineata	3							1			1						1				6
Zonitoides arboreus	73	21	2		1	1	7	16		6	24	8	2	1	1			4	4	2	173
Zonitoides nitidus	5	1					4	3			6	2				1	3	1		3	29
Zoogenetes harpa	6	2						3													11
Species Richness	63	48	16	8	16	20	42	61	8	38	48	49	15	4	32	18	25	44	40	28	

The number of occurrences and absences for each taxon within each area was calculated. Because observed frequencies of taxa were often sparse (< 5) in more than one-fifth of the areas, a log-likelihood ratio test (Zar 1984) was used to identify significant differences in occurrence frequencies. Because this test was repeated on each of the 82 encountered taxa, a Bonferroni correction was used to adjust the significance threshold to 0.000610.

A similar procedure was used to identify which taxa differed in their occurrence frequencies among the five major habitat groups (rock outcrop, upland forest, lowland forest, upland grassland, lowland grassland). The number of occurrences and absences for each taxon within each habitat group was calculated, with the resultant contingency table being analyzed via a log-likelihood ratio test. Again, a Bonferroni correction was used to adjust the significance threshold to 0.000610.

RESULTS

Enumeration of fauna

A total of 82 taxa were identified from the 242 sampled sites. An additional two taxa (*Discus patulus* [Deshayes, 1830] and *Zonitoides limatulus* [W. G. Binney, 1840]) have been previously reported from this region (Levi and Levi 1950, Teskey 1954), but were not relocated during this survey. The total known fauna known from the region is thus 84. The distribution (Table 2), habitat associations (Table 3), and taxonomic considerations (when appropriate) for each of the 82 encountered taxa are detailed in the following alphabetical list. Distribution maps for each (also alphabetically arranged) are found in Appendix I.

Allogona profunda (Say, 1821)

Twenty-seven stations for this species were encountered south and east from the Garden Peninsula. Populations were limited to rock outcrops and upland forests. Complete shells were often difficult to find due to high levels of shrew and rodent predation.

***Anguispira alternata* (Say, 1816)**

This was the most abundant large land snail in the study area (128 sites), being found throughout the region. The great majority of sites occurred on rock outcrops and upland woods. Over 95% of carbonate cliff sites supported populations of this species.

***Carychium exiguum* (Say, 1822)**

Seventy-three stations for this species were encountered throughout the region, with most populations occurring in lowland forests and grasslands. This species is easily distinguished from the following taxon, being consistently wider for a given shell height, even at sites of co-occurrence (Nekola and Barthel 2002).

***Carychium exile* (H. C.Lea, 1842)**

One hundred seven stations were encountered, with occurrence frequencies being highest in the southwest and on the Garden Peninsula. Most populations were found in rock outcrops and upland forests, although it was also found in almost 30% of lowland forests. Morphometric analysis of these populations documented continual variation from small individuals in the southwest to large individuals in the northeast. These data indicate that *Carychium exile canadense* Clapp, 1906 simply represents an endpoint of continuous clinal variation, and does not warrant subspecies designation (Nekola and Barthel 2002).

***Catinella avara* (Say, 1824)**

Nineteen stations for this species were found throughout the region in grasslands and lowland forests. While its shell appeared larger and darker than other members of the genus, the taxonomy of this group (as it true for most Succineids) is made difficult due to extreme plasticity in shell and anatomical morphology. Although Turgeon *et al.* (1998) lump *Catinella avara* into *Catinella vermeta* (Say, 1829), I have chosen to retain *C. avara* due to its long-standing use by North American malacologists (*e.g.*, Baker 1939, Pilsbry 1948, Hubricht 1985), and the use of *C. vermeta* by Frest and Dickson (1986) to designate a different xerophile *Catinella* taxon (see below).

***Catinella exile* (Leonard, 1972)**

Eight stations for this taxon were located throughout the region from lowland grasslands (especially calcareous fens). Diagnostic characteristics are based on Frest (1990), who noted that its shell is smaller, has a higher spire, and is more orange-colored than *Catinella avara*. Described from Pleistocene material, this taxon was previously reported extant only from Iowa fens (Frest, 1990).

***Catinella* cf. *gelida* (F. C. Baker, 1927)**

Nineteen populations for this taxon were found south from Green Bay, with all being limited to rock outcrops. Its shell is smaller than *Catinella avara*, has stronger growth lines, and is of yellowish-green color (Frest 1991). However, it appears essentially identical to *Catinella wandae* (Webb, 1953), which is found in dry, rocky woodlands from eastern Iowa to eastern Oklahoma (Hubricht 1985). No distinguishing features have been provided in the literature (Webb 1953, Frest 1991) to allow separation of these two taxa . Anatomical comparison of *C. wandae* with the type of *Catinella gelida* is not possible, as the latter is a Pleistocene fossil. More anatomical and genetic analysis will be necessary to determine the relationship between these taxa. If valid, *C. gelida* represents a rare Pleistocene relict that was previously reported from only a dozen very small populations in northeastern Iowa and the Black Hills of South Dakota (Frest 1991, Frest and Johannes 1993).

***Catinella* cf. *vermeta* (Say, 1829)**

A single population of this taxon was located on the Maxton Plains Alvar of Drummond Island. It is smaller (< 5 mm tall) and has a deeper suture than *Catinella avara*. I have followed the taxonomic treatment of Frest and Dickson (1986) for these specimens. They reported a similar small, deep-sutured *Catinella* from xeric prairies in western Iowa as *C. vermeta*. Seemingly identical individuals also occur in xeric carbonate glades of northeastern Iowa and southeastern Minnesota (Nekola 2003).

***Cochlicopa lubrica* (Müller, 1774)**

Seventy stations for this taxon were located, with occurrence frequencies being highest in the southwest. Populations were most frequently encountered in upland forests and grasslands. It was especially characteristic of anthropogenically modified habitats such as field-edge stone piles, road verges, and old fields. Following the morphometric analyses of Preece (1992), I have used this name to demarcate individuals with shell heights > 6 mm and widths > 2.3 mm. I have also chosen the European convention (*e.g.*, Kerney and Cameron 1979, Preece 1992, Armbruster 1995) in using *Cochlicopa*, rather than *Cionella* (Turgeon *et al.* 1998), as the generic name for this and the following two taxa.

***Cochlicopa lubricella* (Porro, 1838)**

Thirty-eight stations for this taxon were found throughout the region in a wide variety of habitats. It was most frequently observed in upland forest sites. Kerney and Cameron (1979), Hubricht (1985), and Preece (1992) are followed in using this name to demarcate those mature individuals with shells < 2.3

mm wide and < 6 mm tall. Unlike European populations that are most characteristic of xeric grasslands, the smallest shells were consistently observed from open, calcareous wetlands. Members of this species often co-occurred with *Cochlicopa lubrica*, with intermediate individuals being observed from a number of sites. Additional morphometric and genetic analysis is needed to determine if these taxa are distinct in eastern North America, and if North American populations should be considered synonymous with Eurasian populations.

***Cochlicopa morseana* (Doherty, 1878)**

Twenty-two stations for this taxon were encountered, with occurrence frequencies being highest in the east. Populations were largely limited to cool, mesic rock outcrops and upland forests. This taxon differed from other *Cochlicopa* in the region by possessing tall (> 6 mm) and narrow (< 2.3 mm) shells with flattened whorls (Pilsbry 1948).

***Columella simplex* (Gould, 1841)**

This taxon was found at 130 stations. Populations were most common north and east from Sturgeon Bay. Although observed in almost all habitat types, populations were most often encountered on rock outcrops and upland forests. Live individuals were often observed on low-growing herbs and shrubs, and could be most easily collected through sweep-netting of vegetation. While most populations appeared identical to those figured in Pilsbry (1948), some taller individuals were also found that approached *Columella columella alticola* (Ingerson, 1875) in size, although not in shape. Additional investigations will be necessary to determine the taxonomic status of these populations.

***Deroceras* spp.**

Due to the nature of field collection techniques, live slugs were only infrequently observed. However, internal plates with conspicuous calcareous granules representing *Deroceras* spp. were encountered 67 times from a variety of habitats, particularly to the south of Green Bay. Observations of living individuals suggested that many of the lowland populations represent the native *Deroceras laeve* (Müller, 1774), while upland populations are the introduced *Deroceras reticulatum* (Müller, 1774). The introduced *Arion hortensis* Férussac, 1819 was also frequently observed in upland, wooded sites.

***Discus catskillensis* (Pilsbry, 1898)**

This taxon was observed at 133 stations. It tended to be most frequent northeast of Sturgeon Bay, and showed a strong preference for rock outcrops and upland forests. It also appeared relatively tolerant of anthropogenic disturbance, being frequently present in old fields and field-edge stone piles. Individuals from the far east of the study region (particularly Drummond Island) appeared intermediate with *Discus whitneyi* (Newcomb, 1864). I have also frequently encountered such intermediate individuals in southern Ontario, the Keweenaw Peninsula, and northern Minnesota, suggesting that Pilsbry (1948) may be correct in considering *Discus catskillensis* a subspecies of *D. whitneyi*.

***Discus whitneyi* (Newcomb, 1864) [*Discus cronkhitei*]**

Thirty-four stations for this taxon were encountered throughout the region. Although found in a variety of habitats, populations tended to most frequently occur in lowland grasslands, lowland forests, and upland forests.

***Euchemotrema fraternum* (Say, 1824) [*Stenotrema fraternum*]**

Fifty-five stations for this taxon were found throughout the region. It was most frequently encountered on rock outcrops.

***Euchemotrema leai* (A. Binney, 1841) [*Stenotrema leai*]**

Twenty-eight stations for this taxon were encountered throughout the region. It was most frequently found in lowland grasslands and forests.

***Euconulus alderi* (Gray, 1840)**

Forty-three stations for this taxon were encountered throughout the region, principally from lowland grasslands and forests. Live material was verified as representing this taxon in 1999 by Robert Cameron (pers. comm.). Mature shells were most easily distinguished from *Euconulus fulvus* (Müller, 1774) by being < 2.8 mm in diameter, having a darker-orange color, more glassy luster, and possessing spiral lines on the ventral surface that were more distinct than the transverse lines (Kerney and Cameron 1979). The diameter of the nuclear whorl for *Euconulus alderi* also appeared slightly larger than that of *E. fulvus*. However, in this region *E. alderi* and *E. fulvus* were less distinct than western European populations. The frequency of intermediate individuals appeared low enough, however, to merit maintaining these taxa as separate. Further morphometric and genetic work will be necessary to verify this hypothesis.

***Euconulus fulvus* (Müller, 1774)**

This taxon was observed at 107 stations. Populations tended to be more frequent to the northeast of Sturgeon Bay, and were most often encountered on rock outcrops and upland forests.

***Euconulus polygyratus* (Pilsbry, 1899)**

Fifty-five stations for this taxon were encountered

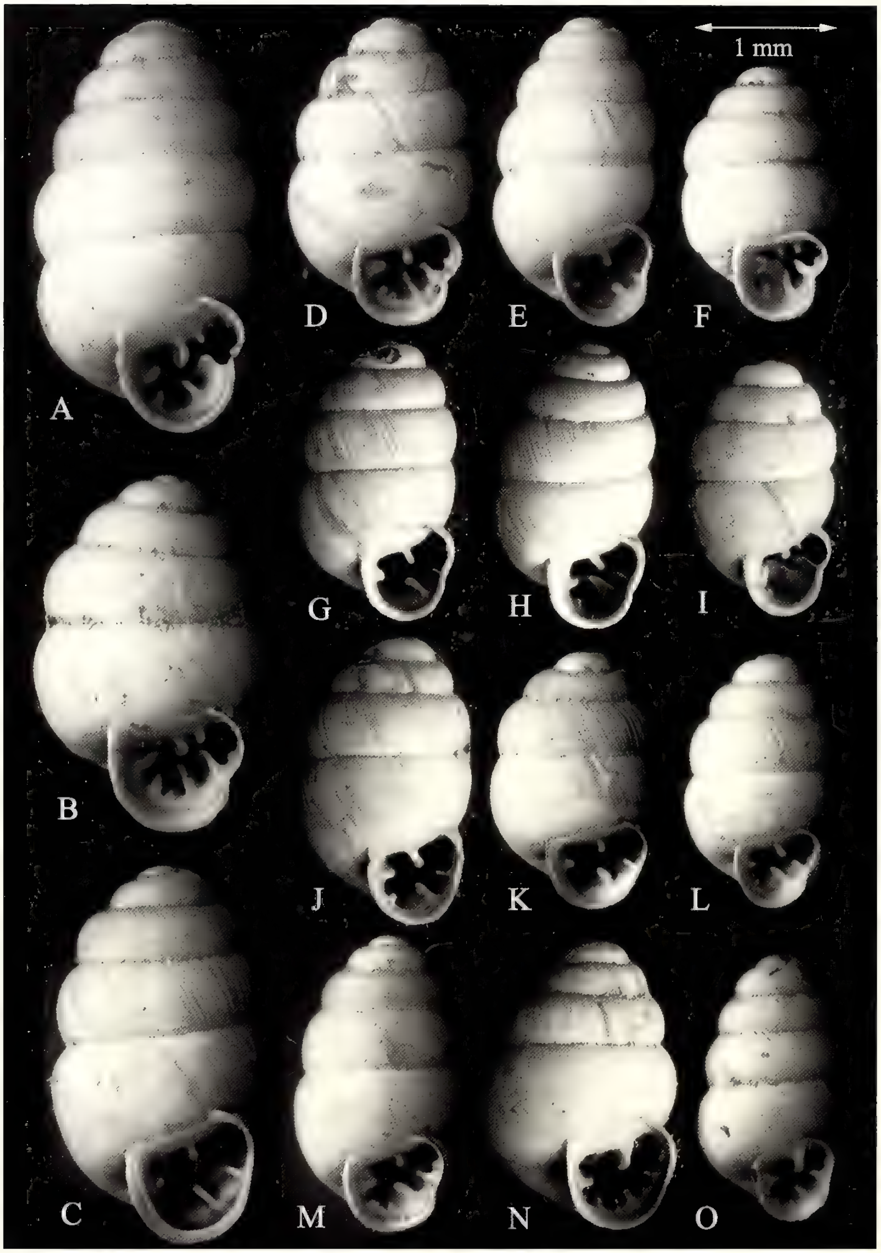

Figure 2. Scanning electron micrographs of selected *Vertigo* and *Gastrocopta* species that occur in the study area. A. *Vertigo morsei*, Summerby Swamp, Mackinac County, Michigan (84°47’43”W, 45°58’15”N), UWGB #3235. B. *Vertigo ovata*, Kimlark Lake, Marinette County, Wisconsin (87°50’56”W, 45°39’37”N), UWGB 1866. C. *Vertigo modesta*, Metcalfe Rock, Grey County, Ontario (80°26’31”W, 44°25’3”N), UWGB 2543. D. *Vertigo elatior*, Allenton Fen, Washington County, Wisconsin (88°18’25”W, 43°22’41”N), UWGB 600. E. *Vertigo tridentata*, Pictured Rocks County Park, Jones County, Iowa (91°6’18”W, 42°12’28”N), UWGB 919. F. *Vertigo milium*, Thiry Daems, Kewaunee County, Wisconsin (87°42’14”W, 44°36’8”N), UWGB 1812. G. *Vertigo paradoxa*, Maple Hill, Chippewa County, Michigan (84°46’55”W, 46°9’34”N), UWGB 2270. H. *Vertigo hubrichti*, Benderville Wayside, Brown County, Wisconsin (87°50’31”W, 44°36’47”N), UWGB 644. I. *Vertigo nylanderi*, Garden Corners, Delta County, Michigan (86°32’4”W, 45°53’23”W), UWGB 2967. J. *Vertigo gouldi*, Toft Point, Door County,Wisconsin (87°5’5”W, 45°4’40”N), UWGB 1062. K. *Vertigo cristata*, Toft Point, Door County, Wisconsin (87°5’5”W, 45°4’40”N), UWGB 1061. L. *Vertigo bollesiana*, Ansel’s Point, Delta County, Michigan (86°34’26”W, 45°48’12”N), UWGB 538. M. *Vertigo pygmaea*, Benderville Wayside, Brown County, Wisconsin (87°50’31”W, 44°36’47”N), UWGB 647. N. *Gastrocopta tappaniana*, Allenton Fen, Washington County, Wisconsin (88°18’25”W, 43°22’41”N), UWGB 590. O. *Gastrocopta pentodon*, Prairie du Rocher, Randolph County, Illinois (90°11’56”W, 38°6’28”N), UWGB 3895.

throughout the region. Populations were most often observed in upland forests and rock outcrops. I have opted to consider *Euconulus polygyratus* as separate from *Euconulus fulvus* due to its slower and more constant rate of increase in whorl width, allowing the body whorl thickness to be less than that of the initial whorls. This species also has pitted transverse lines on the protoconch, giving it a silky luster.

Gastrocopta armifera **(Say, 1821)**

Fifteen stations for this taxon were encountered principally to the south of Green Bay. Populations were largely limited to rock outcrops and upland grasslands. It differed from the closely related *Gastrocopta similis* (Sterki, 1909) by possessing a wider adult shell, a pyramidal columellar lamella, and a taller and thinner lower palatal lamella (Hubricht 1972).

Gastrocopta contracta **(Say, 1822)**

Ninety-nine stations for this taxon were encountered throughout the study region. However, populations were most frequently observed south from the Door Peninsula, and occurred most frequently on rock outcrops and lowland grasslands.

Gastrocopta corticaria **(Say, 1816)**

Thirty-one stations for this taxon were encountered south from the Door Peninsula. Populations were limited to rock outcrops. Some of the populations in the south of the study region possessed between 100-250 individuals per sample.

Gastrocopta holzingeri **(Sterki, 1889)**

Fifty-one stations for this taxon were located. Populations were most frequently observed south from Green Bay, and were most often encountered on rock outcrops and upland grasslands. It was not previously reported from the Upper Peninsula of Michigan (Hubricht 1985).

Gastrocopta pentodon **(Say, 1821)** (Fig. 2O)

Ninety-five stations for this taxon were encountered. Populations tended to be less common in the far east of the study region, and were most often observed on rock outcrops.

Gastrocopta similis **(Sterki, 1909)**

Only a single population of this species was located at the region's most southern rock outcrop where it co-occurred with *Gastrocopta armifera*. It differed from that species by possessing narrower adult shells, a plate-like columellar lamella, and a wide lower palatal lamella inserted more deeply into the aperture than the upper palatal.

Gastrocopta tappaniana **(C. B. Adams, 1842)** (Fig. 2N)

Sixty-seven stations for this taxon were encountered. Although found throughout the region, occurrence frequencies were lowest in the northern Door Peninsula. It was most often observed in lowland grasslands and forests. While occasionally sympatric with *Gastrocopta pentodon* (especially in wooded lowlands), intermediates were not noted.

Glyphyalinia indentata **(Say, 1823)**

Sixty-three stations for this taxon were encountered. Populations tended to be more common towards the southwest, and less common on rock outcrops.

Glyphyalinia rhoadsi **(Pilsbry, 1899)**

Fourteen stations for this taxon were encountered. Populations tended to be more common towards the northeast, and were limited to upland forests and rock outcrops.

Glyphyalinia wheatleyi **(Bland, 1883)**

Only two stations for this taxon were encountered, both from calcareous mesic woods near the Great Lakes shore. One of these sites had been quite heavily disturbed by human activities.

Guppya sterkii **(Dall, 1888)**

Only four stations for this taxon were encountered from rock outcrops and upland forests in proximity to Green Bay. These populations are the most northern yet reported (Hubricht 1985).

Haplotrema concavum **(Say, 1821)**

Five stations for this taxon were encountered from Drummond Island and the south end of Green Bay. Populations were most often found in lowland forests dominated by black ash. Although absent from rock outcrops in eastern Wisconsin, it is abundant on such habitats in northeastern Iowa and northern Illinois (Nekola 2003).

Hawaiia minuscula **(A. Binney, 1840)**

Sixty-nine stations for this taxon were encountered. Populations were most frequently observed to the south of Green Bay in lowland grasslands and rock outcrops.

Helicodiscus parallelus **(Say, 1817)**

Sixty stations for this taxon were encountered across a variety of habitats. Populations were less common in the northern part of the Door Peninsula than elsewhere in the region. Shells of this taxon closely resembled those of *Helicodiscus shimeki*, from which they differed by having wider individual whorls (> 1 mm as measured from the bottom), and relatively deeper and narrower umbilici (Hubricht 1962). Although these two species are usually quite distinct in Wisconsin and the Garden Peninsula, some individuals from the eastern Upper Peninsula appeared intermediate.

Helicodiscus shimeki **Hubricht, 1962**

This taxon was observed at 133 stations throughout the study region. Populations demonstrated a preference for rock outcrops and upland forests.

Hendersonia occulta **(Say, 1831)**

Fifty stations for this taxon were encountered along the Lake Michigan shore from Milwaukee to the northern tip of the Door Peninsula and south along the Niagaran Escarpment to Calumet County. Across this extent, populations tended to favor rock outcrops and upland forests. It is also known from the floodplain of the Escanaba River in Delta County (Pearce *et al.* 1992). It is a common Pleistocene fossil over much of the central US (Hubricht 1985).

Mesodon thyroidus **(Say, 1816)**

Four stations for this taxon were encountered. Populations were restricted to rock outcrops in the northern Door Peninsula.

Neohelix albolabris **(Say, 1816) [*Triodopsis albolabris*]**

Eleven stations for this taxon were encountered. Most populations were located in upland forests on the Door Peninsula. This was the largest species observed during this survey.

Nesovitrea binneyana **(Morse, 1864)**

Fifty stations for this taxon were encountered. Populations became more common towards the northeast, and tended to be most common on rock outcrops.

Nesovitrea electrina **(Gould, 1841)**

Seventy-eight stations for this taxon were encountered throughout the region. Populations were most frequently encountered in lowland grasslands and forests. It was only rarely found sympatric with *Nesovitrea binneyana*.

Novisuccinea ovalis **(Say, 1817) [*Succinea ovalis*]**

Fifty-eight stations for this taxon were encountered in the region. Populations were largely limited to eastern Wisconsin, and tended to be most common in upland forests and rock outcrops.

Oxychilus cellarius **(Müller, 1774)**

Only a single population of this introduced Eurasian species was observed from the region, where it occurred on a wooded limestone talus slope at the northern tip of the Door Peninsula. This population was first located by Robert Cameron (pers. comm.) in September 1999.

Oxychilus draparnaudi **(Beck, 1837).**

Only a single population of this Eurasian species was located in the region, where it occurred on a low limestone outcrop and adjacent rocky roadside. Because this population was centered on a summer vacation house, it is possible that introduction occurred via landscape plantings. This population was also located by Robert Cameron (pers. comm.) in September 1999.

Oxyloma retusa **(I. Lea, 1834)**

Twenty-six stations for this taxon were encountered throughout the region. Most populations occurred in lowland grasslands.

Paravitrea multidentata **(A. Binney, 1840)**

Sixty-eight stations for this taxon were encountered. It became less common south of Sturgeon Bay, and was limited to rock outcrops and upland forests.

Planogyra asteriscus **(Morse, 1857)**

Nine stations for this taxon were encountered. Populations were essentially limited to white cedar-dominated upland and lowland forests in the Upper Peninsula. Although Pilsbry (1948) reported it to be limited to alder thickets, dune slacks, and the wooded margins of *Sphagnum* bogs, I was unable to locate it from such sites.

Pomatiopsis lapidaria **(Say, 1817)**

Four stations for this taxon were encountered. Populations were limited to lowland forests and grasslands. Like Hubricht (1985), I have never encountered this species in an aquatic setting, and feel that it represents a terrestrial species.

Punctum minutissimum **(I. Lea, 1841)**

This taxon was encountered at 133 stations. Populations were largely absent south of Green Bay, and occurred preferentially in rock outcrops and upland forests. Its shells are differentiated those of *Punctum vitreum* H. B. Baker, 1930 by having all ribs of equal size (Pilsbry 1948). Intermediate individuals were infrequently encountered near the southern end of Green Bay.

Punctum vitreum **H. B. Baker, 1930**

Forty-nine stations for this taxon were encountered south from Sturgeon Bay. South of Green Bay it replaces *Punctum minutissimum* as the dominant *Punctum* species of forested habitats. Its shells were distinguished by having every 4th or 5th rib being markedly larger than the intervening ones (Pilsbry 1948). Identification of this species was often made difficult because these larger ribs commonly became worn and almost indistinguishable from the smaller.

***Punctum* n. sp. (*sensu* Frest, 1990)**

This undescribed taxon was encountered at nine stations on the Door Peninsula and the eastern sections of the study region, where it was restricted to lowland grasslands and forests. This taxon was first reported by Frest (1990) from Iowa fens. It differs from *Punctum minutissiumum* and *Punctum vitreum* by having large (> 1.2 mm diameter) and tall (> 0.75 mm) shells with inflated whorls, a narrow umbilicus (< ¼ shell diameter), and a rusty-red color. Additional morphometric and genetic work will be necessary to validate its status.

***Pupilla muscorum* (Linné, 1758)**

Two stations for this taxon were encountered in anthropogenically altered calcareous woodlands from the far east of the study region. This species is more common in southern Ontario, where it occurs in a variety of calcareous upland habitats (Oughton 1948, McMillan *et al.* 2003). It is also well represented in the central US as a Pleistocene fossil (Hubricht 1985).

***Pupoides albilabris* C. B. Adams, 1841**

Only a single population for this taxon was encountered at a calcareous meadow near the south end of Green Bay. This population is disjunct from the southern and central parts of Wisconsin, and represents one of the most northern reported stations. However, as all recovered shells were opaque-white (and long dead), it is possible that this population is no longer extant.

***Stenotrema barbatum* (Clapp, 1904)**

Three stations for this species were observed in the far south of the study region from lowland grasslands and forests.

***Striatura exigua* (Stimpson, 1847)**

Seventy stations for this taxon were encountered. Populations became more common towards the northeast of the study region. It was most often located in lowland forests dominated by tamarack, white cedar, or black ash.

***Striatura ferrea* Morse, 1864**

Forty-one stations for this taxon were encountered. Populations became more frequent towards the northeast of the study region, and were essentially limited to forests. South of Sturgeon Bay, it was limited to rich, lowland forests.

***Striatura milium* (Morse, 1859)**

This taxon was observed at 125 stations. Populations became more common in occurrence towards the north, and were most often located in lowland forests. In the north it replaced *Punctum minutissimum* as the most common disk-shaped micro-snail. In the south it was less common and limited to rich, wooded wetlands.

***Strobilops aenea* Pilsbry, 1926**

A single colony of this species was located in the study area from a mesic, wooded limestone talus slope along the east shore of Green Bay where it was found crawling on coarse woody debris after a rain. This population was discovered by Brian Coles (pers. comm.) in July 1999. It was previously reported in the region from Peninsula State Park, approximately 20 km north (Levi and Levi 1950). These populations represent this species known northern range limit, and are likely disjunct from northeastern Iowa (Hubricht 1985).

***Strobilops affinis* Pilsbry, 1893**

Nineteen stations for this taxon were encountered from grasslands and lowland forests. Except for a lone colony in a fen near the Mackinac Straits, populations were limited to the south of Sturgeon Bay.

***Strobilops labyrinthica* (Say, 1817)**

This species was found at 176 stations. Although most frequently encountered in rock outcrops and upland forests to the north of Green Bay, it was found throughout the study region from most surveyed habitat types.

***Vallonia costata* (Müller, 1774)**

Forty-one stations for this taxon were encountered, primarily west from the Garden Peninsula. While found in a wide variety of habitats, it appeared quite tolerant of human disturbance, being characteristic on calcareous roadsides, old fields, and stonepiles.

***Vallonia excentrica* Sterki, 1893**

Only three stations for this taxon were encountered in upland habitats south from Sturgeon Bay. These sites (representing abandoned agricultural fields and stonepiles) have been subjected to high levels of human disturbance. Mature shells of this species are most easily separated from those of *Vallonia pulchella* (Müller, 1774) by their yellowish color, smoother surface, and minor axis diameter of 1½ mm or less (Gerber 1996).

***Vallonia gracilicosta* Reinhardt, 1883**

Thirty-two stations for this taxon were encountered throughout the region from rock outcrops. Occurrences of this species follow the Niagaran Escarpment and adjacent carbonate outcrops from southeastern Minnesota to southern Ontario. It is an abundant late Pleistocene fossil throughout central North America (Hubricht 1985).

Vallonia perspectiva **Sterki, 1892**

Twelve stations for this taxon were encountered south from Lake Winnebago, principally from rock outcrops. These populations often produced over 250 shells per sample.

Vallonia pulchella **(Müller, 1774)**

Twenty-nine stations for this taxon were encountered. Populations were confined to the west of the Mackinac Straits, and tended to be most common in grasslands. It was often present in sites that had been subjected to intense levels of anthropogenic disturbance. Its shells were differentiated from the similar *Vallonia excentrica* by their white color, distinct growth lines, and minor axis diameter of 1½ mm or more (Gerber 1996).

Vertigo bollesiana **(Morse, 1865)** (Fig. 2L)

Seventy-three stations for this taxon were encountered. Populations were most frequently observed from rock outcrops and upland forests on the Door Peninsula. Shells from populations located from lowland habitats appeared more narrow and striate than those from upland habitats.

Vertigo cristata **(Sterki, 1919)** (Fig. 2K)

Twenty-five stations for this clearly-marked species (Nekola 2001) were encountered. It was confined to rock outcrops and forests north of 45ºN. No intermediates between it and either *Vertigo gouldi* (A. Binney, 1843) or *Vertigo paradoxa* Sterki, 1900 were noted, even at sites of co-occurrence.

Vertigo elatior **Sterki, 1894** (Fig. 2D)

Fifty-eight stations for this taxon were encountered throughout the region. Populations were largely limited to lowland forests and grasslands, where this taxon became the most common *Vertigo* species. It is an abundant late Pleistocene fossil in the central USA (Frest and Dickson 1986).

Vertigo gouldi **(A. Binney, 1843)** (Fig. 2J)

This taxon was found at 123 stations throughout the region, where it represented the most frequently occurring *Vertigo* species. While most often observed on rock outcrops, it was also occasionally located in upland and lowland forests.

Vertigo hubrichti (Pilsbry, 1934) (Fig. 2H)

Seventy-three stations for this taxon were encountered. Populations were largely limited to rock outcrops, and were most frequently seen on the Door and Garden Peninsulas. This species was first described as a Pleistocene fossil, but was subsequently found alive at approximately 50 sites in the Paleozoic Plateau of northeastern Iowa, southwestern Wisconsin, and southeastern Minnesota (Frest 1991). It is differentiated from *Vertigo paradoxa* Sterki, 1900 by having a strong basal lamella, a more deeply inserted lower palatal lamella, and a deeper depression on the outside of the shell over the lower palatal lamella (Pilsbry 1948, Frest 1991). However, individuals appearing intermediate between it and *V. paradoxa* were also observed throughout the eastern Upper Peninsula and southern Ontario. While morphometric and genetic analysis across the geographic ranges of both taxa will be necessary to determine their status, these preliminary observations suggest that *Vertigo hubrichti* may be best regarded as a subspecies of *V. paradoxa* that is currently limited to the vicinity of the western Lake Michigan shore and the upper Mississippi River valley.

Vertigo milium **(Gould, 1840)** (Fig. 2F)

Forty sites for this taxon were encountered. This species was essentially limited to sites south of Sturgeon Bay, where it was found across a wide variety of habitats. It reached its highest population densities (> 300 per sample) on calcareous open meadows and fens.

Vertigo modesta **(Say, 1824)** (Fig. 2C)

A single population of this species was located in northeastern Wisconsin, where individuals occurred in leaf litter accumulations under car-sized boulders on a natural, glacially deposited rock pile. This habitat is insulated from summer warmth, with ice persisting until June. The nearest known extant colonies occur approximately 150 km to the north on the northern tip of the Keweenaw Peninsula, 250 km to the northwest on the north shore of Lake Superior in northeastern Minnesota, and 300 km to the east on Manitoulin Island (Nekola *et al.* 1999). All other reported central USA occurrences for this taxon are Pleistocene fossils (Hubricht 1985).

Vertigo morsei **Sterki, 1894** (Fig. 2A)

Six stations for this taxon were encountered. Although populations were scattered throughout the region, they were all limited to calcareous fens supporting loose accumulations of bryophytes and dead sedge leaves over the ground surface. In Iowa, this species is also very rare and limited to fens (Frest 1990).

Vertigo nylanderi **Sterki, 1909** (Fig. 2I)

Seventeen stations for this taxon were encountered throughout the region. Populations were essentially limited to rich lowland forests, and were typically dominated by tamarack or black ash. Fewer than 5 mature individuals were secured from all but 2 sites. The only other reports of this species are from Maine, Ontario, Michigan, and northwestern Minnesota (Oughton 1948, Pilsbry 1948, Dawley 1955, Burch and Jung 1988, Pearce *et al.* 1992, Nekola and Massart 2001). It is also known from Pleistocene sediments in central Illinois (Frest 1991, Miller *et al.* 1994), and Holocene sediments from southern Ontario (Rich Meyrick pers. comm.).

Vertigo ovata **Say, 1822** (Fig. 2B)

Twenty-three stations for this taxon were encountered throughout the region. Populations were limited to lowland grasslands and forests.

***Vertigo paradoxa* Sterki, 1900** (Fig. 2G)

Eighteen stations for this taxon were encountered. Populations became more common towards the east and tended to occur most often in soil pockets on mesic, wooded cliffs. It largely replaced *Vertigo hubrichti* east of Schoolcraft County. *Vertigo paradoxa* was previously reported in the eastern USA only from northern Maine, the northern Lower Peninsula of Michigan, and the Black Hills of South Dakota (Frest and Johannes 1993). It is a wide-ranging fossil from Pleistocene sediments in the central USA (Frest and Johannes 1993).

***Vertigo pygmaea* (Draparnaud, 1801)** (Fig. 2M)

Thirty-five stations for this taxon were encountered across a wide variety of habitats. Populations were more frequently encountered south of Sturgeon Bay and were often observed in areas subjected to high levels of anthropogenic disturbance.

***Vertigo tridentata* Wolf, 1870** (Fig. 2E)

Five stations for this taxon were located on rock outcrops south of Green Bay. These populations are the most northern yet reported (Hubricht 1985).

***Vitrina limpida* Gould, 1850**

Seventeen stations for this taxon were encountered. Populations were found in a wide variety of habitats, and became more common towards the east. In the west of the study region, it appeared limited to sites near to the Lake Michigan shore. It also appeared able to tolerate fairly high levels of anthropogenic disturbance.

***Webbhelix multilineata* (Say, 1821) [*Triodopsis miltilineata*]**

Six stations for this taxon were observed from Sturgeon Bay to Lake Winnebago in a variety of habitats.

***Zonitoides arboreus* (Say, 1816)**

One hundred and seventy-three stations for this taxon were encountered throughout the region. Although found in almost every habitat type, it was most frequently located on rock outcrops and lowland forests. Only rarely were more than a dozen mature shells secured from a single site.

***Zonitoides nitidus* (Müller, 1774)**

Twenty-nine stations for this taxon were encountered from a wide variety of habitats. Populations were largely limited to sites south from the Door Peninsula, where they appeared tolerant of anthropogenic disturbance.

***Zoogenetes harpa* (Say, 1824)**

Eleven stations for this taxon were encountered. Populations occurred more frequently to the northeast, and were limited to rock outcrops and upland forests.

Excluded Species

Two taxa previously reported from the region were considered to be erroneously reported by earlier workers. *Mesodon pennsylvanicus* (Green, 1827) was listed from Marinette County by Jass (1986). This report (and all others in that paper) is based upon specimen identifications made by Leslie Hubricht during the mid-1980's. I have found specimens identified during this time in the Hubricht Collection at FMNH to be commonly misidentified. As neither this species, nor other extralimital taxa (*Triodopsis tridentata* [Say, 1816], *Triodopsis vulgata* Pilsbry, 1940) reported by Jass (1986) from just beyond the study region were located during this more exhaustive survey, I have chosen to consider these reports as unreliable.

Additionally, Hubricht (1985) reports *Vertigo ventricosa* (Morse, 1865) from Mackinac County. My observations of material at FMNH have shown this species to be commonly misidentified by Hubricht and others. Shells of *V. ventricosa* differ from those of *Vertigo pygmaea* and *Vertigo elatior* by having an aperture that is approximately ⅓ of the shell height, a weak sinulus, a very weak (or absent) callus between the palatal lamellae, a weak crest, very weak to absent striae, and an almost transparent shell of light brown color (Pilsbry 1948). I have not yet observed this suite of characteristics from any individual collected west of central New York State. *Vertigo ventricosa* appears to possess a narrow range extending from Newfoundland to West Virginia along the crest of the Appalachians, therefore I have chosen to consider all reports of this species from the western Great Lakes to be based on misidentifications.

Species richness patterns

The number of species encountered per county was found to differ substantially (Table 2). Door County had the maximum number of observed taxa at 70, followed by Brown (63), Delta (57), Chippewa (55), Manitowoc (53), Calumet (51), and Mackinac (50). The lowest richness levels were (not surprisingly) limited to counties with only single collection sites, including Washington (19), Green Lake (17), and Langlade (12).

The number of encountered species was also found to differ among habitat types (Table 3). Carbonate cliffs and rocky woodlands harbored the greatest number of species (63 and 61, respectively), accounting for approximately 75% of the regional fauna. Lakeshore carbonate ledges, lakeshore woodlands, tamarack wetlands, white cedar wetlands, fens, and calcareous meadows were found to harbor between 49-40 taxa (58%-48% of the regional total). The most depauperate fauna was that of sand dunes, where only 4 taxa were observed (5% of total).

Table 4. Occurrence frequency for each taxa within five geographic subregions. Area 1 (51 sites) ranges from Lake Winnebago and south. Area 2 (64 sites) ranges from Sturgeon Bay and southern Oconto County to the north side of Lake Winnebago. Area 3 (74 sites) ranges from from Rock Island and Marinette County to Sturgeon Bay and central Oconto County. Area 4 (23 sites) ranges across Delta and Schoolcraft counties, including all of the Garden Peninsula. Area 5 (30 sites) ranges from Drummond Island west to central Mackinac counties. P-values are based on log-likelihood ratio contengency table analyses, with bold-faced entries representing those taxa demonstrating significant deviation from equal frequencies across all geographic areas. The significance threshold was modified, using a Bonferroni correction, to p = 0.000610.

Taxa	Occurrence Frequency					
	Area 1	Area 2	Area 3	Area 4	Area 5	p
Allogona profunda	**27.45**	**6.25**	**10.81**	**4.35**	**0.00**	**0.000397**
Anguispira alternata	49.02	46.88	59.46	56.52	53.33	0.618003
Carychium exiguum	23.53	45.31	24.32	21.74	30.00	0.046232
Carychium exile	49.02	57.81	35.14	52.17	23.33	0.007238
Catinella avara	9.80	12.50	2.70	13.04	3.33	0.123466
Catinella exile	5.88	0.00	2.70	4.35	6.67	0.187976
Catinella* cf. *gelida	**27.45**	**7.81**	**0.00**	**0.00**	**0.00**	**0.000000**
Catinella cf. *vermeta*	0.00	0.00	0.00	0.00	3.33	0.378966
Cochlicopa lubrica	**47.06**	**37.50**	**14.86**	**17.39**	**23.33**	**0.000534**
Cochlicopa lubricella	15.69	28.13	9.46	13.04	6.67	0.024425
Cochlicopa morseana	1.96	6.25	8.11	17.39	23.33	0.016082
Columella simplex	**23.53**	**42.19**	**71.62**	**69.57**	**73.33**	**0.000000**
***Deroceras* spp.**	**47.06**	**34.38**	**16.22**	**26.09**	**10.00**	**0.000297**
Discus catskillensis	37.25	43.75	68.92	65.22	66.67	0.001033
Discus whitneyi	19.61	21.88	4.05	13.04	13.33	0.015699
Euchemotrema fraternum	29.41	12.50	25.68	17.39	30.00	0.126935
Euchemotrema leai	15.69	17.19	8.11	8.70	3.33	0.174227
Euconulus alderi	19.61	20.31	13.51	17.39	20.00	0.831441
Euconulus fulvus	33.33	34.38	56.76	47.83	50.00	0.035898
Euconulus polygyratus	11.76	21.88	25.68	26.09	33.33	0.176595
Gastrocopta armifera	11.76	12.50	1.35	0.00	0.00	0.002200
Gastrocopta contracta	49.02	54.69	36.49	26.09	20.00	0.004581
Gastrocopta corticaria	**33.33**	**14.06**	**6.76**	**0.00**	**0.00**	**0.000002**
Gastrocopta holzingeri	**39.22**	**35.94**	**8.11**	**8.70**	**0.00**	**0.000000**
Gastrocopta pentodon	33.33	48.44	44.59	43.48	13.33	0.007738
Gastrocopta similis	1.96	0.00	0.00	0.00	0.00	0.536340
Gastrocopta tappaniana	**29.41**	**45.31**	**12.16**	**21.74**	**30.00**	**0.000483**
Glyphyalinia indentata	9.80	28.13	29.73	30.43	36.67	0.026584
Glyphyalinia rhoadsi	0.00	4.69	5.41	8.70	16.67	0.026496
Glyphyalinia wheatleyi	0.00	0.00	1.35	0.00	3.33	0.433273
Guppya sterkii	0.00	3.13	1.35	4.35	0.00	0.388246
Haplotrema concavum	0.00	6.25	0.00	0.00	3.33	0.040479
Hawaiia minuscula	**49.02**	**48.44**	**6.76**	**21.74**	**10.00**	**0.000000**
Helicodiscus parallelus	**27.45**	**35.94**	**5.41**	**21.74**	**43.33**	**0.000008**
Helicodiscus shimeki	43.14	54.69	64.86	56.52	40.00	0.077097
Hendersonia occulta	**19.61**	**43.75**	**16.22**	**0.00**	**0.00**	**0.000000**
Mesodon thyroidus	0.00	0.00	5.41	0.00	0.00	0.047091
Neohelix albolabris	1.96	0.00	12.16	0.00	3.33	0.002886
Nesovitrea binneyana	**7.84**	**10.94**	**20.27**	**26.09**	**60.00**	**0.000001**
Nesovitrea electrina	25.49	40.63	29.73	30.43	20.00	0.260305
Novisuccinea ovalis	**33.33**	**35.94**	**22.97**	**4.35**	**0.00**	**0.000005**
Oxychilus cellarius	0.00	0.00	1.35	0.00	0.00	0.666393
Oxychilus draparnaudi	0.00	0.00	1.35	0.00	0.00	0.666393
Oxyloma retusa	13.73	15.63	5.41	13.04	6.67	0.266881
Paravitrea multidentata	**3.92**	**23.44**	**41.89**	**34.78**	**40.00**	**0.000005**
Planogyra asteriscus	**0.00**	**0.00**	**1.35**	**13.04**	**16.67**	**0.000255**
Pomatiopsis lapidaria	3.92	1.56	1.35	0.00	0.00	0.560707
Punctum minutissimum	**1.96**	**42.19**	**81.08**	**86.96**	**83.33**	**0.000000**
Punctum n. sp.	9.80	1.56	4.05	0.00	0.00	0.066742
Punctum vitreum	**56.86**	**31.25**	**0.00**	**0.00**	**0.00**	**0.000000**
Pupilla muscorum	0.00	0.00	0.00	0.00	6.67	0.075778

Table 4. (continued)

Taxa			**Occurrence Frequency**			
	Area 1	Area 2	Area 3	Area 4	Area 5	p
Pupoides albilabris	0.00	1.56	0.00	0.00	0.00	0.614180
Stenotrema barbatum	5.88	0.00	0.00	0.00	0.00	0.050049
Striatura exigua	**1.96**	**25.00**	**35.14**	**26.09**	**70.00**	**0.000000**
Striatura ferrea	**1.96**	**10.94**	**20.27**	**21.74**	**43.33**	**0.000026**
Striatura milium	**17.65**	**48.44**	**62.16**	**73.91**	**73.33**	**0.000000**
Strobilops aenea	0.00	0.00	1.35	0.00	0.00	0.666393
Strobilops affinis	9.80	17.19	2.70	0.00	3.33	0.005728
Strobilops labyrinthica	**47.06**	**76.56**	**82.43**	**78.26**	**80.00**	**0.000401**
Vallonia costata	**23.53**	**28.13**	**9.46**	**17.39**	**0.00**	**0.000328**
Vallonia excentrica	3.92	1.56	0.00	0.00	0.00	0.274481
Vallonia gracilicosta	9.80	10.94	16.22	13.04	16.67	0.789687
Vallonia perspectiva	**23.53**	**0.00**	**0.00**	**0.00**	**0.00**	**0.000000**
Vallonia pulchella	15.69	21.88	6.76	8.70	0.00	0.003467
Vertigo bollesiana	**7.84**	**32.81**	**54.05**	**21.74**	**10.00**	**0.000000**
Vertigo cristata	**0.00**	**0.00**	**20.27**	**13.04**	**23.33**	**0.000000**
Vertigo elatior	21.57	28.13	17.57	30.43	30.00	0.462544
Vertigo gouldi	45.10	45.31	59.46	52.17	50.00	0.448656
Vertigo hubrichti	**11.76**	**20.31**	**50.00**	**47.83**	**16.67**	**0.000002**
Vertigo milium	**27.45**	**39.06**	**1.35**	**0.00**	**0.00**	**0.000000**
Vertigo modesta	0.00	0.00	1.35	0.00	0.00	0.666393
Vertigo morsei	1.96	0.00	4.05	0.00	6.67	0.160618
Vertigo nylanderi	5.88	12.50	1.35	8.70	10.00	0.080021
Vertigo ovata	11.76	6.25	13.51	8.70	3.33	0.385160
Vertigo paradoxa	**0.00**	**0.00**	**8.11**	**17.39**	**26.67**	**0.000004**
Vertigo pygmaea	**19.61**	**32.81**	**4.05**	**0.00**	**3.33**	**0.000001**
Vertigo tridentata	7.84	1.56	0.00	0.00	0.00	0.034972
Vitrina limpida	**3.92**	**3.13**	**1.35**	**17.39**	**26.67**	**0.000224**
Webbhelix multilineata	7.84	3.13	0.00	0.00	0.00	0.034572
Zonitoides arboreus	58.82	71.88	81.08	56.52	80.00	0.028374
Zonitoides nitidus	23.53	15.63	6.76	4.35	3.33	0.012781
Zoogenetes harpa	**0.00**	**0.00**	**1.35**	**17.39**	**20.00**	**0.000015**

Occurrence Frequency *vs.* Geography

Thirty-one of the encountered taxa were found to vary significantly in their occurrence frequencies across the study region (Table 4). Fourteen (*Allogona profunda*, *Catinella* cf. *gelida*, *Cochlicopa lubrica*, *Deroceras* spp., *Gastrocopta corticaria*, *Gastrocopta holzingeri*, *Hawaiia minuscula*, *Hendersonia occulta*, *Novisuccinea ovalis*, *Punctum vitreum*, *Vallonia costata*, *Vallonia perspectiva*, *Vertigo milium*, *Vertigo pygmaea*) increased in occurrence frequency toward the southwest. Another 13 (*Columella simplex*, *Nesovitrea binneyana*, *Paravitrea multidentata*, *Planogyra asteriscus*, *Punctum minutissimum*, *Striatura exigua*, *Striatura ferrea*, *Striatura milium*, *Strobilops labyrinthica*, *Vertigo cristata*, *Vertigo paradoxa*, *Vitrina limpida*, *Zoogenetes harpa*) increased in frequency towards the northeast. *Vertigo bollesiana* and *Vertigo hubrichti* had their highest occurrence frequencies along the Door and Garden Peninsulas, while *Gastrocopta tappaniana* and *Helicodiscus parallelus* had their minimum occurrence frequencies in this same region.

A number of other taxa also demonstrated non-significant, but possibly important, trends in occurrence frequency. Many of these taxa did not attain statistically significant trends in their distributions due to their reduced occurrences. Species that tended towards greater occurrence frequency in the south and west included *Gastrocopta armifera*, *Gastrocopta contracta*, *Gastrocopta pentodon*, *Gastrocopta similis*, *Stenotrema barbatum*, *Strobilops affinis*, *Vallonia excentrica*, *Vertigo tridentata*, and *Webbhelix multilineata*. Species that tended towards greater occurrence frequency in the north and east included *Discus catskillensis*, *Glyphyalinia indentata*, *Glyphyalinia rhoadsi*, and *Pupilla muscorum*. Species that tended towards highest occurrence frequencies in the Door and Garden Peninsulas included *Guppya sterkii*, *Mesodon thyroidus*, *Neohelix albolabris*, *Oxychilus cellarius*, *Oxychilus draparnaudi*, and *Strobilops aenea*.

Occurrence Frequency *vs.* Habitat

Forty-one species demonstrated significant variation in their occurrence frequencies among the five habitat groups

Table 5. Occurrence frequency for each taxon within five general habitat groupings. Group 1 consists of Rock Outcrops (RO; 107 sites). Group 2 consists of Upland Forests (UF; 44 sites). Group 3 consists of Lowland Forests (LF; 48 sites). Group 4 consists of Upland Grasslands (UG; 10 sites). Group 5 consists of Lowland Grasslands (LG; 33 sites). P-values are based on log-likelihood ratio contengency table analyses, with bold-faced entries representing those taxa demonstrating significant deviation from equal frequencies across all habitat groupings. The significance threshold was modified, using a Bonferroni correction, to p = 0.000610.

Taxa	Occurrence Frequency				
	RO	UF	LF	UG	LG	p
Allogona profunda	**20.56**	**11.36**	**0.00**	**0.00**	**0.00**	**0.000006**
Anguispira alternata	**92.52**	**56.82**	**6.25**	**0.00**	**3.03**	**0.000000**
Carychium exiguum	**3.74**	**6.82**	**83.33**	**10.00**	**75.76**	**0.000000**
Carychium exile	**59.81**	**43.18**	**29.17**	**50.00**	**15.15**	**0.000013**
Catinella avara	0.93	0.00	12.50	40.00	24.24	0.000000
Catinella exile	0.00	0.00	0.00	0.00	24.24	0.000001
Catinella* cf. *gelida	**17.76**	**0.00**	**0.00**	**0.00**	**0.00**	**0.000001**
Catinella cf. *vermeta*	0.00	0.00	0.00	10.00	0.00	0.166558
Cochlicopa lubrica	**26.17**	**59.09**	**12.50**	**40.00**	**18.18**	**0.000015**
Cochlicopa lubricella	17.76	22.73	4.17	10.00	18.18	0.068383
Cochlicopa morseana	10.28	18.18	4.17	0.00	3.03	0.055085
Columella simplex	**70.09**	**61.36**	**29.17**	**20.00**	**36.36**	**0.000001**
Deroceras spp.	33.64	11.36	25.00	0.00	42.42	0.000883
Discus catskillensis	**89.72**	**50.00**	**20.83**	**10.00**	**12.12**	**0.000000**
Discus whitneyi	9.35	15.91	18.75	10.00	21.21	0.341968
Euchemotrema fraternum	**45.79**	**11.36**	**2.08**	**0.00**	**0.00**	**0.000000**
Euchemotrema leai	**0.93**	**2.27**	**20.83**	**10.00**	**45.45**	**0.000000**
Euconulus alderi	**0.00**	**2.27**	**50.00**	**0.00**	**54.55**	**0.000000**
Euconulus fulvus	**62.62**	**45.45**	**20.83**	**20.00**	**24.24**	**0.000001**
Euconulus polygyratus	**30.84**	**36.36**	**6.25**	**10.00**	**6.06**	**0.000040**
Gastrocopta armifera	12.15	2.27	0.00	10.00	0.00	0.001711
Gastrocopta contracta	**60.75**	**18.18**	**25.00**	**10.00**	**39.39**	**0.000000**
Gastrocopta corticaria	**28.97**	**0.00**	**0.00**	**0.00**	**0.00**	**0.000000**
Gastrocopta holzingeri	**41.12**	**6.82**	**4.17**	**20.00**	**0.00**	**0.000000**
Gastrocopta pentodon	**64.49**	**18.18**	**27.08**	**30.00**	**6.06**	**0.000000**
Gastrocopta similis	0.93	0.00	0.00	0.00	0.00	0.802044
Gastrocopta tappaniana	**2.80**	**11.36**	**60.42**	**50.00**	**75.76**	**0.000000**
Glyphyalinia indentata	38.32	22.73	10.42	30.00	12.12	0.000701
Glyphyalinia rhoadsi	8.41	11.36	0.00	0.00	0.00	0.007192
Glyphyalinia wheatleyi	0.93	2.27	0.00	0.00	0.00	0.683532
Guppya sterkii	2.80	2.27	0.00	0.00	0.00	0.426856
Haplotrema concavum	0.93	2.27	6.25	0.00	0.00	0.251832
Hawaiia minuscula	36.45	15.91	18.75	10.00	39.39	0.009955
Helicodiscus parallelus	23.36	25.00	35.42	20.00	18.18	0.442604
Helicodiscus shimeki	**79.44**	**54.55**	**27.08**	**20.00**	**15.15**	**0.000000**
Hendersonia occulta	**28.97**	**29.55**	**10.42**	**0.00**	**3.03**	**0.000110**
Mesodon thyroidus	3.74	0.00	0.00	0.00	0.00	0.157759
Neohelix albolabris	5.61	11.36	0.00	0.00	0.00	0.016560
Nesovitrea binneyana	31.78	13.64	10.42	20.00	9.09	0.003708
Nesovitrea electrina	**7.48**	**6.82**	**79.17**	**40.00**	**63.64**	**0.000000**
Novisuccinea ovalis	28.97	36.36	10.42	10.00	15.15	0.009486
Oxychylus cellarius	0.00	2.27	0.00	0.00	0.00	0.488870
Oxychilus draparnaudi	0.93	0.00	0.00	0.00	0.00	0.802044
Oxyloma retusa	**0.93**	**0.00**	**12.50**	**10.00**	**54.55**	**0.000000**
Paravitrea multidentata	**52.34**	**27.27**	**0.00**	**0.00**	**0.00**	**0.000000**

Table 5. (continued)

Taxa	**Occurrence Frequency**					
	RO	UF	LF	UG	LG	p
Planogyra asteriscus	2.80	4.55	6.25	0.00	3.03	0.759055
Pomatiopsis lapidaria	0.00	0.00	4.17	0.00	6.06	0.060175
Punctum minutissimum	**69.16**	**59.09**	**35.42**	**40.00**	**36.36**	**0.000180**
***Punctum* n. sp.**	**0.00**	**0.00**	**6.25**	**0.00**	**18.18**	**0.000117**
Punctum vitreum	27.10	20.45	20.83	0.00	3.03	0.002837
Pupilla muscorum	0.00	2.27	2.08	0.00	0.00	0.419751
Pupoides albilabris	0.00	0.00	0.00	0.00	3.03	0.404473
Stenotrema barbatum	0.00	0.00	2.08	0.00	6.06	0.111997
Striatura exigua	**20.56**	**29.55**	**58.33**	**0.00**	**21.21**	**0.000006**
Striatura ferrea	16.82	22.73	25.00	0.00	3.03	0.010618
Striatura milium	**48.60**	**50.00**	**81.25**	**10.00**	**33.33**	**0.000003**
Strobilops aenea	0.93	0.00	0.00	0.00	0.00	0.802044
Strobilops affinis	**0.00**	**0.00**	**18.75**	**10.00**	**27.27**	**0.000000**
Strobilops labyrinthica	**93.46**	**52.27**	**66.67**	**50.00**	**48.48**	**0.000000**
Vallonia costata	18.69	11.36	8.33	40.00	24.24	0.077704
Vallonia excentrica	0.00	2.27	0.00	20.00	0.00	0.012558
Vallonia gracilicosta	**29.91**	**0.00**	**0.00**	**0.00**	**0.00**	**0.000000**
Vallonia perspectiva	10.28	2.27	0.00	0.00	0.00	0.004560
Vallonia pulchella	7.48	9.09	6.25	30.00	33.33	0.001871
Vertigo bollesiana	**56.07**	**18.18**	**10.42**	**0.00**	**0.00**	**0.000000**
Vertigo cristata	**19.63**	**4.55**	**4.17**	**0.00**	**0.00**	**0.000204**
Vertigo elatior	**0.00**	**6.82**	**60.42**	**20.00**	**72.73**	**0.000000**
Vertigo gouldi	**96.26**	**31.82**	**12.50**	**0.00**	**0.00**	**0.000000**
Vertigo hubrichti	**64.49**	**6.82**	**0.00**	**10.00**	**0.00**	**0.000000**
Vertigo milium	17.76	4.55	22.92	10.00	21.21	0.079342
Vertigo modesta	0.00	2.27	0.00	0.00	0.00	0.488870
Vertigo morsei	**0.00**	**0.00**	**0.00**	**0.00**	**18.18**	**0.000052**
Vertigo nylanderi	**0.00**	**4.55**	**31.25**	**0.00**	**0.00**	**0.000000**
Vertigo ovata	**0.00**	**0.00**	**12.50**	**0.00**	**51.52**	**0.000000**
Vertigo paradoxa	14.02	4.55	2.08	0.00	0.00	0.003858
Vertigo pygmaea	14.02	13.64	2.08	30.00	30.30	0.003276
Vertigo tridentata	4.67	0.00	0.00	0.00	0.00	0.081368
Vitrina limpida	3.74	15.91	2.08	40.00	3.03	0.001113
Webbhelix multilineata	2.80	2.27	2.08	0.00	3.03	0.960081
Zonitoides arboreus	**89.72**	**56.82**	**83.33**	**20.00**	**30.30**	**0.000000**
Zonitoides nitidus	5.61	15.91	16.67	10.00	21.21	0.066758
Zoogenetes harpa	7.48	6.82	0.00	0.00	0.00	0.030018

(Table 5). These patterns were less easy to categorize, with species tending to possess more individualistic relationships. However, three main response types were noted. Fifteen taxa (*Carychium exiguum, Catinella exile, Euchemotrema leai, Euconulus alderi, Gastrocopta tappaniana, Nesovitrea electrina, Oxyloma retusa, Punctum* n. sp., *Striatura exigua, Striatura milium, Strobilops affinis, Vertigo elatior, Vertigo morsei, Vertigo nylanderi, Vertigo ovata*) possessed highest occurrence frequencies in lowland grasslands and/or forests. Thirteen taxa (*Anguispira alternata, Catinella* cf. *gelida, Discus catskillensis, Euchemotrema fraternum, Gastrocopta corticaria, Gastrocopta holzingeri, Gastrocopta pentodon, Strobilops labyrinthica, Vallonia gracilicosta, Vertigo bollesiana, Vertigo cristata, Vertigo gouldi, Vertigo hubrichti*) were most commonly encountered on rock outcrops. Nine others (*Allogona profunda, Columella simplex, Euconulus fulvus, Euconulus polygyratus, Helicodiscus shimeki, Hendersonia occulta, Paravitrea multidentata, Punctum minutissimum*) were found most frequently in both rock outcrops and upland forests.

DISCUSSION

The 82 taxa encountered from the 242 sample sites represent over 50% of the taxa previously reported from Illinois, Indiana, Iowa, Michigan, Minnesota, southern Ontario, and Wisconsin, and 15% of the taxa reported from eastern North America (Oughton 1948, Pilsbry 1948, Burch 1962, Hubricht 1985).

Some of these have rather limited ranges in the eastern USA (Pilsbry 1948, Hubricht 1985, Frest 1991, Nekola 2001, Nekola and Massart 2001). *Catinella exile* is otherwise known only from Iowa fens. *Catinella* cf. *gelida* is otherwise limited to limestone cliff and talus slopes in northeastern Iowa and the Black Hills. *Hendersonia occulta* is otherwise limited to the Ridge and Valley province in the central and southern Appalachians, and to the Paleozoic Plateau in the Upper Midwest. *Planogyra asteriscus* is otherwise known only from northern New England and the upper Great Lakes. *Strobilops affinis* is otherwise found from eastern Minnesota to Missouri, the southern Great Lakes shore, and eastern Massachusetts. *Vallonia gracilicosta* is otherwise known in eastern North America from isolated populations confined to carbonate outcrops from the Paleozoic Plateau eastward along the Niagaran Escarpment to central New York State, eastern Maine, and Massachusetts. *Vertigo bollesiana* is otherwise limited to the New England states south along the Appalachians and Allegheny Plateau to western North Carolina and west along the Great Lakes to southeastern Michigan. *Vertigo cristata* is otherwise known from northern Wisconsin, northern Minnesota, and the western Upper Peninsula of Michigan. *Vertigo hubrichti* was previously known only from algific talus slopes in the Paleozoic Plateau. *Vertigo modesta* was previously reported from the eastern US only as a Pleistocene fossil, although extant colonies have recently been documented from northern Minnesota and Michigan. *Vertigo morsei* was known from scattered fens extending from Iowa and Minnesota through the southern Great Lakes to central New York State. *Vertigo nylanderi* was otherwise known only from northern Maine, northeastern Ontario, the northern Lower Peninsula of Michigan, and northwestern Minnesota. *Vertigo paradoxa* was otherwise known only from northern Maine, the northern Lower Peninsula of Michigan, and the Black Hills. *Zoogenetes harpa* was otherwise known only from the northern Great Lakes and northern New England.

Species Richness Patterns

A substantial amount of the observed diversity in land snails in the region is maintained at relatively small geographic scales, with up to 80% of the regional fauna being recorded from a single county (Door). Individual 1000 m^2 areas within the region are capable of supporting up to 34 taxa, or 40% of the regional fauna (Nekola 1999), while some 400 cm^2 areas within these sites may harbor up to 21 co-occurring taxa, or 25% of the regional fauna (Nekola and Smith 1999). The mechanisms that allow for these levels of mycrosympatry are not yet fully elucidated.

The bulk of species richness also occured within a relatively small subset of habitats that included carbonate cliffs, lakeshore carbonate ledges, rocky woodlands, forested wetlands (black ash, tamarack, or black spruce), and fens. These habitats individually harbored from 50-75% of the entire regional fauna. Only 2 of the encountered taxa (*Catinella* cf. *vermeta*, *Pupoides albilabris*) were not located within at least one of these habitats. These same habitat types are also among the most important for land snail diversity in northwestern Europe (Kerney and Cameron 1979).

Biogeographic Patterns and Affinities

A clear trend in faunistic composition was found across the region, with 14 taxa being more common to the southwest and 13 more common to the northeast. This result is not unexpected, as this region straddles the Northern and Eastern Provinces of the Eastern North American Molluscan Division. However, these data demonstrate that this transition is not abrupt, with faunistic turnover occurring over the region's entire 250 km extent.

The biogeographic affinities of species sharing a given occurrence pattern within the region are also not uniform. While many Interior Province taxa were more common in the southwest (*e.g.*, *Allogona profunda*, *Gastrocopta armifera*, *Gastrocopta contracta*, *Gastrocopta corticaria*, *Gastrocopta holzingeri*, *Gastrocopta pentodon*, *Gastrocopta similis*, *Hawaiia minuscula*, *Stenotrema barbatum*, *Strobilops affinis*, *Vallonia perspectiva*, *Vertigo milium*, *Vertigo tridentata*, *Webbhelix multilineata*), and many of the Northern Province forms were more common to the northeast (*e.g.*, *Discus catskillensis*, *Nesovitrea binneyana*, *Planogyra asteriscus*, *Pupilla muscorum*, *Striatura exigua*, *Striatura milium*, *Vertigo cristata*, *Vertigo paradoxa*, *Vitrina limpida*, *Zoogenetes harpa*), not all within-region distributions reflected such larger-scale patterns. For instance, *Cochlicopa lubrica*, *Novisuccinea ovalis*, *Vallonia costata*, *Vallonia pulchella*, *Vallonia excentrica*, *Vertigo pygmaea* are all species characteristic of the northeastern US (Hubricht 1985), yet reached their greatest occurrence frequency in the southwest of the study region. Additionally, *Glyphyalinia rhoadsi*, *Paravitrea multidentata*, and *Striatura ferrea* reached their greatest occurrence frequencies in the northeast of the region, even though their ranges are primarily centered on the Appalachians (Hubricht 1985). *Columella simplex*, *Punctum minutissimum*, and *Strobilops labyrinthica* are all wide ranging species of the eastern US (Hubricht, 1985), yet reached their peak occurrence frequencies in the northeast of the region.

Those species reaching their peak abundances along the Door and Garden Peninsulas also proved to have diverse affinities. *Mesodon thyroidus* is found throughout the eastern US, while *Neohelix albolabris* and *Vertigo bollesiana* are limited to the northeastern US. *Guppya sterkii* and *Strobilops aenea*, however, are characteristic of the southeastern US. *Vertigo hubrichti* represents an upper Midwestern endemic. Such patterns help demonstrate that the transition from Interior to Northern Province faunas in the region is not only diffuse, but also complex.

Conservation Recommendations

Only 3 species with more than 20 occurrences (*Glyphyalinia indentata*, *Cochlicopa lubricella*, and *Discus whitneyi*) possessed statistically similar frequencies across all habitat groups and geographic subregions. All remaining taxa demonstrated either significant partitioning across space and/or environment, or were too scarce (< 20 occurrences) to provide reliable results due to low statistical power.

These data suggest that conservation of land snail richness and compositional diversity within the region will require the protection of multiple habitat types across the entire landscape. Given the high number of species that they harbor, carbonate cliffs, rocky upland woods, wooded wetlands (black ash, tamarack, white cedar), and fens should be given particular consideration. By protecting representative examples of these habitats within each of the geographic subregions, roughly 97% of the regional land snail diversity could be conserved.

However, some of these habitats are experiencing severe losses within parts of the region. For instance, most of the carbonate cliffs in eastern Wisconsin have already been altered or are currently under threat from development, road construction, and/or grazing. Unless conservation groups and agencies take immediate action to protect such sites across the region, irrevocable losses in land snail diversity may occur.

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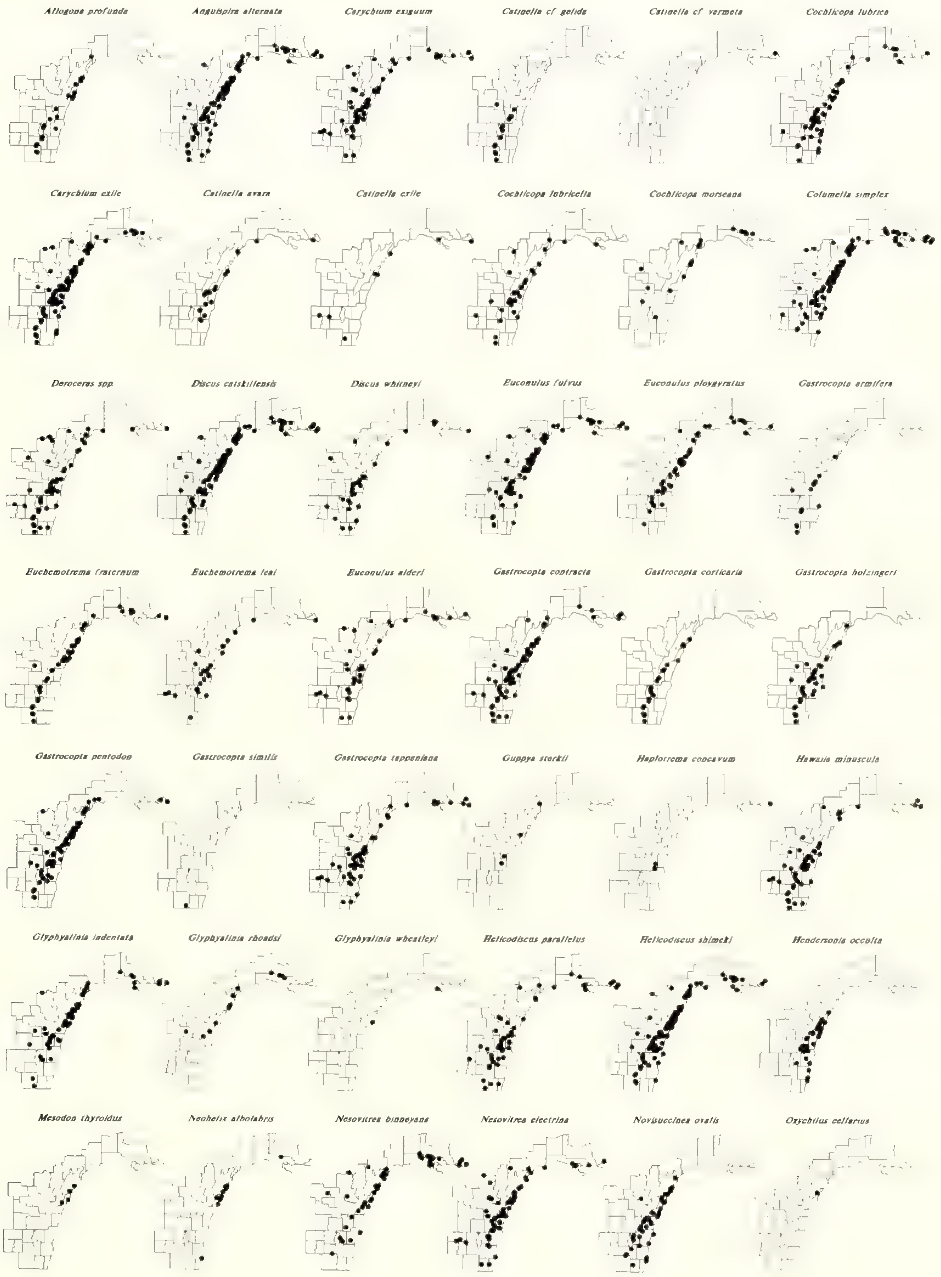
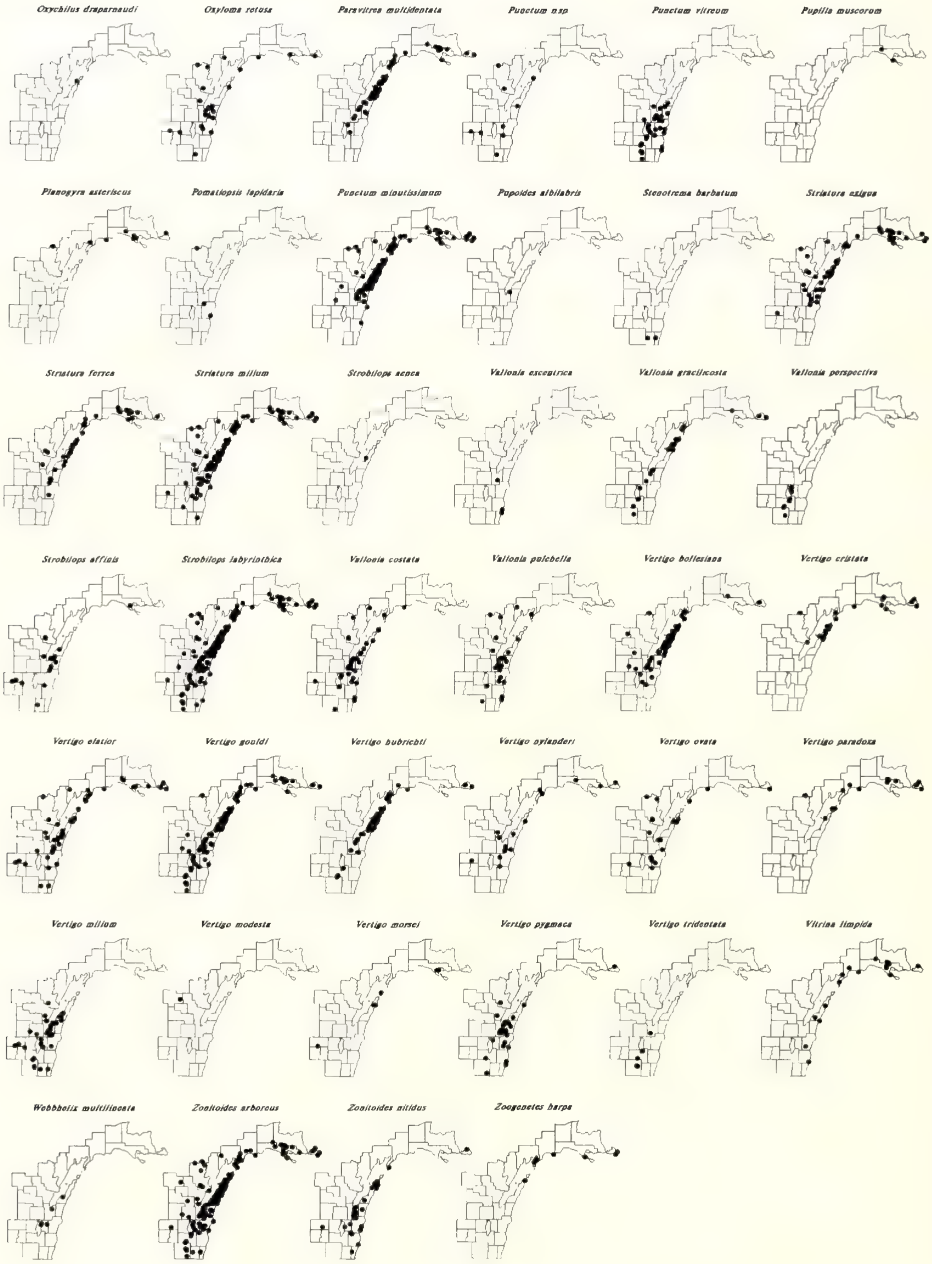
APPENDIX 1

Distribution maps for all species encountered within all 242 sites sampled within the study region. Species maps are alphabetically arranged.



Allogona profunda
Anguispira alternata
Carychium exiguum
Catinella cf gelida
Catinella cf vermeta
Cochlicopa lubrica
Carychium exile
Catinella avara
Catinella exile
Cochlicopa lubricella
Cochlicopa morseana
Columella simplex
Deroceras spp.
Discus catskillensis
Discus whitneyi
Euconulus fulvus
Euconulus ploygyratus
Gastrocopta armifera
Euchemotrema fraternum
Euchemotrema leai
Euconulus alderi
Gastrocopta contracta
Gastrocopta corticaria
Gastrocopta holzingeri
Gastrocopta pentodon
Gastrocopta similis
Gastrocopta tappaniana
Guppya sterkii
Haplotrema concavum
Hawaiia minuscula
Glyphyalinia indentata
Glyphyalinia rhoadsi
Glyphyalinia wheatleyi
Helicodiscus parallelus
Helicodiscus shimeki
Hendersonia occulta
Mesodon thyroidus
Neohelix albolabris
Nesovitrea binneyana
Nesovitrea electrina
Novisuccinea ovalis
Oxychilus cellarius

APPENDIX 1 (continued)



Oxychilus draparnaudi
Oxyloma retusa
Paravitrea multidentata
Punctum n.sp
Punctum vitreum
Pupilla muscorum
Planogyra asteriscus
Pomatiopsis lapidaria
Punctum minutissimum
Pupoides albilabris
Stenotrema barbatum
Striatura exigua
Striatura ferrea
Striatura milium
Strobilops aenea
Vallonia excentrica
Vallonia gracilicosta
Vallonia perspectiva
Strobilops affinis
Strobilops labyrinthica
Vallonia costata
Vallonia pulchella
Vertigo bollesiana
Vertigo cristata
Vertigo elatior
Vertigo gouldi
Vertigo hubrichti
Vertigo nylanderi
Vertigo ovata
Vertigo paradoxa
Vertigo milium
Vertigo modesta
Vertigo morsei
Vertigo pygmaea
Vertigo tridentata
Vitrina limpida
Webbhelix multilineata
Zonitoides arboreus
Zonitoides nitidus
Zoogenetes harpa

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Sexual dimorphism in *Lampsilis siliquoidea* (Barnes, 1823) (Bivalvia: Unionidae)

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Abstract: To test for sexual dimorphism in *Lampsilis siliquoidea*, we collected data on total length, height, width, anterior-to-beak length, thickness of the right valve, presence of color rays, and sex from shells of specimens collected across Wisconsin, between 1973 and 1977. Based on the means of these measurements, females were smaller than males. However, detailed statistical analysis of female/male differences in size and shape revealed a more complex relationship between these factors and provided an in-depth view of sexual dimorphism in this species, in contrast to prior simplified generalizations in the literature on this topic.

Keywords: Wisconsin, shell morphometrics

Lampsilis siliquoidea (Barnes, 1823) is by far the most abundant and widely distributed unionid in Wisconsin. Mathiak's (1979) five-year survey of waterways in the state ranked it first in total number of specimens collected (n = 1161) and in number of localities at which it was found (n = 236).

Cummings and Mayer (1992) provided a succinct summary of the biology and life history of the freshwater mussels of the Midwest. The reproductive cycle of unionids includes a phase in which the fertilized eggs develop into glochidia and are stored internally in portions of the gills of the female that function as brood chambers. In some species of freshwater bivalves, morphological differences between males and females are also reflected in distinctive shell traits. One such unionid is *Lampsilis siliquoidea*, or fatmucket (Turgeon *et al.* 1998). The fatmucket was originally described from Wisconsin, with the type locality given as the Wisconsin River.

Defined taxonomically as a member of the tribe Lampsilini (Burch 1975), in which sexual dimorphism is often very marked, female shells of this species show obvious posterior inflation, which accommodates the distension and enlargement of the gills when they are filled with eggs. All members of the genus *Lampsilis* have the marsupium, or egg-filled region, restricted to the outer pair of gills only, a condition which places them with several other genera in the subgroup Heterogenae (Burch 1975). Females of the Lampsilini are gravid year round except in the summer months. Data from Baker (1928) indicate that each gravid female fatmucket may contain 15-40 ovisacs, and that each young mussel in the glochidium stage is 0.25 mm x 0.29 mm in size. In contrast to that of the female, the male shell is less inflated and is bluntly pointed rather than evenly rounded posteriorly. In addition to these shape differences, Baker (1928) generalized that the shells of male *Lampsilis siliquoidea* are usually larger than those of females. Our purpose was to test this generalization by conducting a more detailed morphometric analysis of measurements made on a larger sample of Wisconsin members of this species than had been examined in the past.

METHODS

During the summers of 1973 to 1977, Mathiak (1979) surveyed 641 localities on 251 Wisconsin rivers and creeks for unionid mussels. Drought conditions from 1975 to mid-1977 caused exceptionally low water levels, facilitating collecting. To collect specimens, Mathiak waded into the water (up to depths of 1.2 m) and used a pitchfork with a curved piece of 25 mm-meshed welded fabric wired across the tines to collect unionids.

Shells of *Lampsilis siliquoidea* from the Mathiak study (Fig. 1) were chosen for the current morphometric analysis. The Milwaukee Public Museum (MPM) subset of the Mathiak collection includes 121 specimens of *L. siliquoidea* that each measure over 66 mm in total length. Baker (1928) gave that as the length he considered the minimum for sexual maturity in this species.

Data on seven shell traits were gathered for each specimen: (1) total length, (2) height, (3) width, (4) anterior-to-beak length of the right valve, (5) thickness of the right valve (at the juncture of the pallial line with the anterior muscle scar), (6) presence or absence of color rays, and (7) sex (based on shell shape). Morphometric traits 1-5 were measured to the nearest 0.1 mm with a dial caliper. Numeric data were analyzed using SYSTAT software (Version 10.2). An analysis of covariance was conducted to test the validity of female/male differences. The $p \leq 0.05$ level was that chosen for significance in all statistical testing.

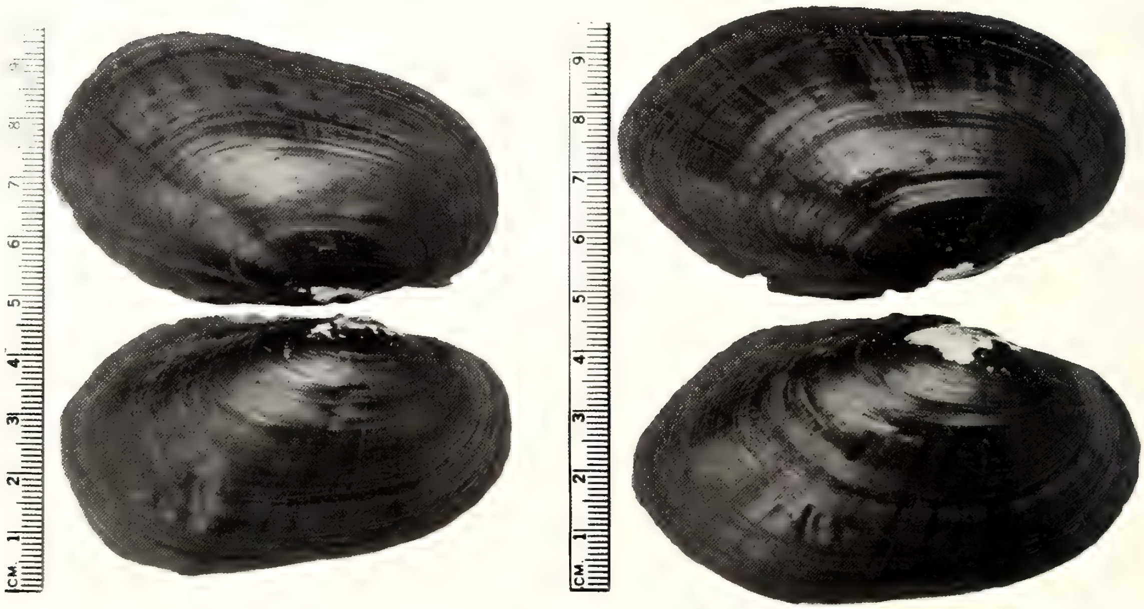

Figure 1. *Lampsilis siliquoidea* collected by H. A. Mathiak from the East Fork of the Black River, Jackson County, Wisconsin, June 2, 1976. Left, female, Right, male. Note the posterior inflation and evenly rounded posterior margin of the female shell.

RESULTS

Males dominated the upper range of length measurements. Of 121 shells measured, 84.6% of specimens longer than 95.0 mm were male. Below that upper range, differences in female/male proportions in size can be seen by comparing the measurements from eleven same-length specimen pairs. In these pairs, 82.0% of the females had greater heights and widths than same-length males. Similar percentages of females (81.0%) and males (77.1%) were rayed.

Descriptive statistics for both males and females are given in Table 1. The means for all male variables exceed those for females. Variation about the means is inconsequential, the coefficients of variation being < 1%, with the most variable measurement being male shell thickness. This table also shows that the significant positive correlation of male variables with length is stronger than that for female variables (male r = 0.75-0.96, female r = 0.69-0.94). Three male variables (height, width, anterior-to-beak length) were related to length in a manner that is linear (r > 0.90) or nearly so, whereas only the first two variables have this relationship to length in the females. Similarly, the slopes of the log-log regressions on length were closer to 1.0 for male than for female variables.

Table 1. Measurements of shells of *Lampsilis siliquoidea*. (Var., variable; LF, length of females; HF, height of females; WF, width of females; AF, anterior-to-beak length of females; TF, thickness of females; LM, length of males; HM, height of males; WM, width of males; AM, anterior-to-beak length of males; TM, thickness of males; SD, standard deviation; SE, standard error; Min., minimum; Max., maximum; CV, coefficient of variation; b, slope; a, intercept; r, correlation coefficient, $p < 0.05$; *n*, number of individuals).

Sample statistics Females *n* = 39, Males *n* = 82							Regresssion statistics Variable on L			Log on Log L		
Var.	Mean	SD	SE	Min.	Max.	CV	b	a	r	b	a	r
LF	81.3	11.5	1.8	67.7	113.2	0.2	--	--	--	--	--	--
HF	48.4	8.0	1.3	40.2	80.0	0.2	0.65	-4.76	0.94	1.05	-0.33	0.95
WF	30.7	5.9	1.0	21.8	48.0	0.2	0.45	-5.93	0.88	1.18	-0.78	0.88
AF	21.3	3.8	0.6	9.8	30.9	0.2	0.26	0.25	0.78	1.04	-0.65	0.70
TF	3.7	0.9	0.1	2.1	5.3	0.2	0.05	-0.56	0.69	1.23	-1.79	0.67
LM	87.0	14.9	1.6	66.4	133.2	0.2	--	--	--	--	--	--
HM	48.7	7.4	0.8	37.5	73.7	0.2	0.48	7.20	0.96	0.87	0.01	0.97
WM	31.2	6.7	0.7	22.2	53.6	0.2	0.41	-4.55	0.92	1.09	-0.63	0.91
AM	21.8	5.0	0.6	11.2	38.0	0.2	0.30	-4.32	0.89	1.17	-0.93	0.87
TM	3.9	1.4	0.2	1.9	9.6	0.4	0.07	-2.05	0.75	1.46	-2.26	0.74

Table 2 presents the results for analysis of covariance of the male and the female slopes when plotting $\log_{10}$ of length against the $\log_{10}$ values for height, width, anterior-to-beak length, and thickness. When reported in terms of the resulting least squares mean values, male slopes differ significantly from those for females. All differences are significant at values well below the 0.05 level chosen for statistical significance, except for the $\log_{10}$ thickness comparison whose p value = 0.09.

Table 2. Adjusted least squares means for the slopes of male and female $\log_{10}$ variables plotted against their $\log_{10}$ lengths.

Variable		Mean	Std. Error
Log_{10} Height			
	F	1.697	0.003
	M	1.675	0.002
Log_{10} Width			
	F	1.501	0.006
	M	1.475	0.004
Log_{10} Anterior			
	F	1.342	0.009
	M	1.316	0.006
Log_{10} Thickness			
	F	0.582	0.015
	M	0.551	0.010

DISCUSSION

Baker (1928) made the general statement that *Lampsilis siliquoidea* females were the smaller sex, basing this on a set of 3 measurements taken from 9 Wisconsin specimens. We calculated means for his data and found that males (n = 6) do exceed females (n = 3) in terms of length (99.8 mm versus 82.3 mm) and height (54.2 mm versus 51.7 mm). The third measurement Baker reported is diameter, which he defined (Baker 1898) as the distance between the valves at their widest part (thus corresponding to our "width"). The mean diameter of Baker's Wisconsin females, 41.7 mm, is larger than that for males, 38.7 mm.

Baker (1928) made similar measurements for three additional subspecies: *Lampsilis siliquoidea pepinensis* F. C. Baker, 1927 (3 males, 3 females), *L. siliquoidea rosacea* (De Kay, 1843) (3 males, 3 females) and *L. siliquoidea chadwicki* F. C. Baker, 1928 (2 males, 2 females). The only two cases in which the means of the female shells exceeded those of the males are for diameters of *L. siliquoidea pepinensis* and *L. siliquoidea chadwicki.*

Baker (1898) presented the three measurements for 5 (2 male, 3 female) fatmucket specimens from Illinois (though the scientific name he gave for the species was *Lampsilis luteolus* Lamarck, 1818). In each of these cases, the mean measurements of male shells are less than those of females.

Kesler and Manning (1996) measured shell lengths of males and females from a fatmucket population in the Wolf River in Mississippi and Tennessee and found females to be longer.

In contrast to the simpler, straightforward statements about *Lampsilis siliquoidea* found in some literature of the past (Baker 1928), our morphometric analysis has revealed the complexity of the relationship between shape and size in this species and indicates that similar parameters should be included in future studies exploring sexual dimorphism in bivalves. The combination of physiological studies in the laboratory with additional long-term life history studies of specific populations would undoubtedly enhance our understanding of sexual dimorphism in this common freshwater unionid. While a major portion of the sexual dimorphism in the size and shape of the shells of *L. siliquoidea* is due to the reproductive biology of the female, whose posteriorly inflated shell accommodates the marsupium, no doubt other traits, such as differences in rates of growth and life span, may also influence shell morphology.

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Morphology of the penial hooks and vaginal cuticular lining of some dorid nudibranchs (Mollusca, Opisthobranchia)

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Abstract: The penis and vagina of *Otinodoris winckworthi* and *Platydoris* spp. were examined with the aid of a scanning electron microscope. These taxa have vaginas lined by a cuticle and their penises bear wide and short penial hooks. In *O. winckworthi* the cuticle is relatively smooth and has holes that may be caused by the penetration of the penial hooks during copulation. This is supported by the fact that the diameter of the holes is similar to the diameter of the tips of the penial hooks of the same specimen. In *Platydoris* spp. the vaginal cuticle is very folded, sometimes armed with hooks, and was not penetrated by the penial hooks during copulation in the specimens examined. The presence of a cuticular lining on the vagina may provide a better anchorage for the penial hooks of the partner during copulation in larger species of dorid nudibranchs.

Key words: Doridacea, *Otinodoris*, *Platydoris*, reproductive interaction.

Dorid nudibranchs are a highly diverse group of opisthobranch mollusks. As in most members of the Opisthobranchia, dorids are simultaneous hermaphrodites, with sperm being exchanged by both partners during copulation (Hadfield and Switzer-Dunlap 1984). The male system matures first, and fully mature individuals function as male and female (Gosliner 1994).

The penis of a dorid nudibranch consists of a cirrus that is housed within the muscular portion of the deferent duct. The penis everts during copulation by pleuremboly (Evans 1914, Marcus 1955: fig. 132), probably as a consequence of the perfusion of blood from the hemocoel into the loose fibrous tissue surrounding the penis (Evans 1914), so that the innermost wall of the relaxed penis is extruded and becomes the external wall of the erected penis. The proximal end of the penis becomes the distal end when the process is complete. Therefore, the penial hooks, which are proximally oriented, are exposed during the eversion process, rolling in a radiating fashion (Rivest 1984, García and García-Gómez 1989). The function of the penial hooks is probably to anchor the penis inside the vagina of the partner to prevent premature separation if one of the partners is disturbed (Rivest 1984, García and García-Gómez 1989). In dorid nudibranchs there are two main types of penial hooks. The first type includes fragile-looking hooks, characterized by having an elongate cusp and a thin base, but there is a large variability in shape between species. Fragile-looking hooks are present in numerous groups of dorids (Valdés and Gosliner 1999, Valdés and Gosliner 2001). In comparison, the second type of hook, present in species of *Gargamella*, *Baptodoris*, *Platydoris*, and *Otinodoris*, are more solid, with a thick, rounded base and a strong triangular cusp (Gosliner 1991, Ballesteros and Valdés 1999, Garovoy *et al.* 1999). Penial hooks are not present in all dorid nudibranchs, so their function appears not to be critical for reproduction. In a few rare cases, the penial hooks are used to tear a hole in the body of the partner to incite copulation (Rivest 1984).

The distal portion of the vagina of some dorid nudibranchs is lined by a cuticle. Several species that have a cuticular lining also have vaginal hooks or spines. Schmekel and Portmann (1982) described the presence of a heavily folded cuticle, armed with hooks, in the distal region of the vagina of *Platydoris argo* (Linnaeus, 1767). Gosliner (1994) mentioned the presence of this lining and vaginal hooks in species of the genera *Carminodoris* and *Artachaea*, but neither study provides more detailed morphological information. Nothing has been published on the ultrastructure, chemical composition, or function of this vaginal lining.

The present paper provides morphological information and discusses the possible function of the vaginal lining in some species of the genera *Platydoris* and *Otinodoris* and its interaction with penial hooks during copulation.

MATERIALS AND METHODS

Several specimens belonging to the genera *Platydoris* Bergh, 1877 and *Otinodoris* White, 1948 were examined (Table 1). They included one representative of each of the following species: *Platydoris argo* (Linnaeus, 1767), *Platydoris scabra* (Cuvier, 1804), *Platydoris cruenta* (Quoy and Gaimard, 1832), *Platydoris angustipes* (Mörch, 1863), *Platydoris formosa*

Table 1. Material examined for the present study.

Species	Catalogue number	Locality	Length (preserved)
Platydoris argo (Linnaeus, 1767)	CASIZ 115217	Cabo de Palos, Murcia, Spain	70 mm
Platydoris scabra (Cuvier, 1804)	CASIZ 057684	Tutuila Island, American Samoa	92 mm
Platydoris cruenta (Quoy and Gaimard, 1832)	CASIZ 071600	Madang, Papua New Guinea	67 mm
Platydoris angustipes, (Mörch, 1863)	CASIZ 072295	Grand Bahama Island, Bahamas	42 mm
Platydoris formosa (Alder and Hancock, 1864)	CASIZ 110432	Batangas, Luzon, Philippines	69 mm
Otinodoris winckworthi White, 1948	CASIZ 073238	Île Saint Marie, Madagascar	155 mm

(Alder and Hancock, 1864), and *Otinodoris winckworthi* White, 1948. Specimens were identified using features of the radula, reproductive system, and external morphology. All specimens studied were deposited in the Department of Invertebrate Zoology of the California Academy of Sciences (CASIZ).

Specimens were collected in the field and preserved in Bouin's solution. After approximately two weeks in Bouin's, they were transferred to 75% ethanol. Specimens were dissected and their reproductive systems removed. This was facilitated by first making a dorsal incision on the preserved animals. The muscular portion of the deferent duct and the vagina were isolated from the remainder of the reproductive system. These organs were cut longitudinally and opened to expose the penial hooks and vaginal lining. They were mounted on scanning electron microscope (SEM) stubs previously covered with double-faced tape, and kept open until they dried. The mounted samples were sputtered coated for 200 seconds with gold/paladium and examined with a SEM (Leo 1430VP).

RESULTS

The cuticular vaginal lining in a single specimen of *Otinodoris winckworthy* was relatively smooth and shiny when observed with SEM (Fig. 1A). It had several irregular folds and low ridges. A close examination showed the presence of numerous small holes in the cuticular surface (Fig. 2B). These holes were oval (Fig. 2C) and similar in size, about 6-7 μm in maximum diameter. The diameters of the holes found in *O. winckworthy* were similar to the diameters of the tips of the penial hooks in the same specimen (Fig. 2A). The specimen examined had a higher density of holes in the vagina (about 10 per 500 μm^2) than the tips of the penial hooks in the same specimen (about 4 per 500 μm^2). All of the holes were located less than 150 μm from each other, whereas the tips of the penial hooks were separated by a wider distance (more than 200 μm). The cuticular lining in all species of *Platydoris* studied was very different from that of *Otinodoris winckworthy*. In *Platydoris* spp. the cuticle had numerous deep pitches and folds (Fig. 1B-D). In a few species large vaginal hooks were present (Fig. 1D). The specimen of *Platydoris formosa* had a number of ridges that were varied in width and length and were arranged in an irregular pattern (Fig. 1B). In *Platydoris scabra* the ridges appeared to be aligned parallel to the walls of the vagina and crossed by irregular pitches and folds (Fig. 1C). The vagina of *Platydoris angustipes* had several large hooks surrounded by a number of irregular ridges (Fig. 1D). In all species of *Platydoris* examined the vaginal surface was in general rougher than that of *O. winckworthy*. Vaginal linings of five species of *Platydoris* were examined specifically looking for holes, but in no case were holes observed.

DISCUSSION

Function and shape of penial hooks

The fragile-looking penial hooks of most dorid nudibranchs should be able to penetrate easily the soft tissue that lines the vagina to anchor the penis. The thinner and longer the penial hooks are, the deeper they should penetrate the vaginal tissue and anchor the penis.

In animals with a vaginal cuticular lining, the penial hooks should be wider and shorter to perform the anchoring function without breaking apart in the process. In fact, the penial hooks of species having cuticular vaginal linings are shorter and wider than in other groups of dorids (Gosliner 1991, Ballesteros and Valdés 1999, Garovoy *et al.* 1999, Valdés and Gosliner 2001, Dorgan *et al.* 2002, present study). This direct relationship between the shape of the penial hooks and the presence of a cuticular lining in the vagina suggests a functional relationship.

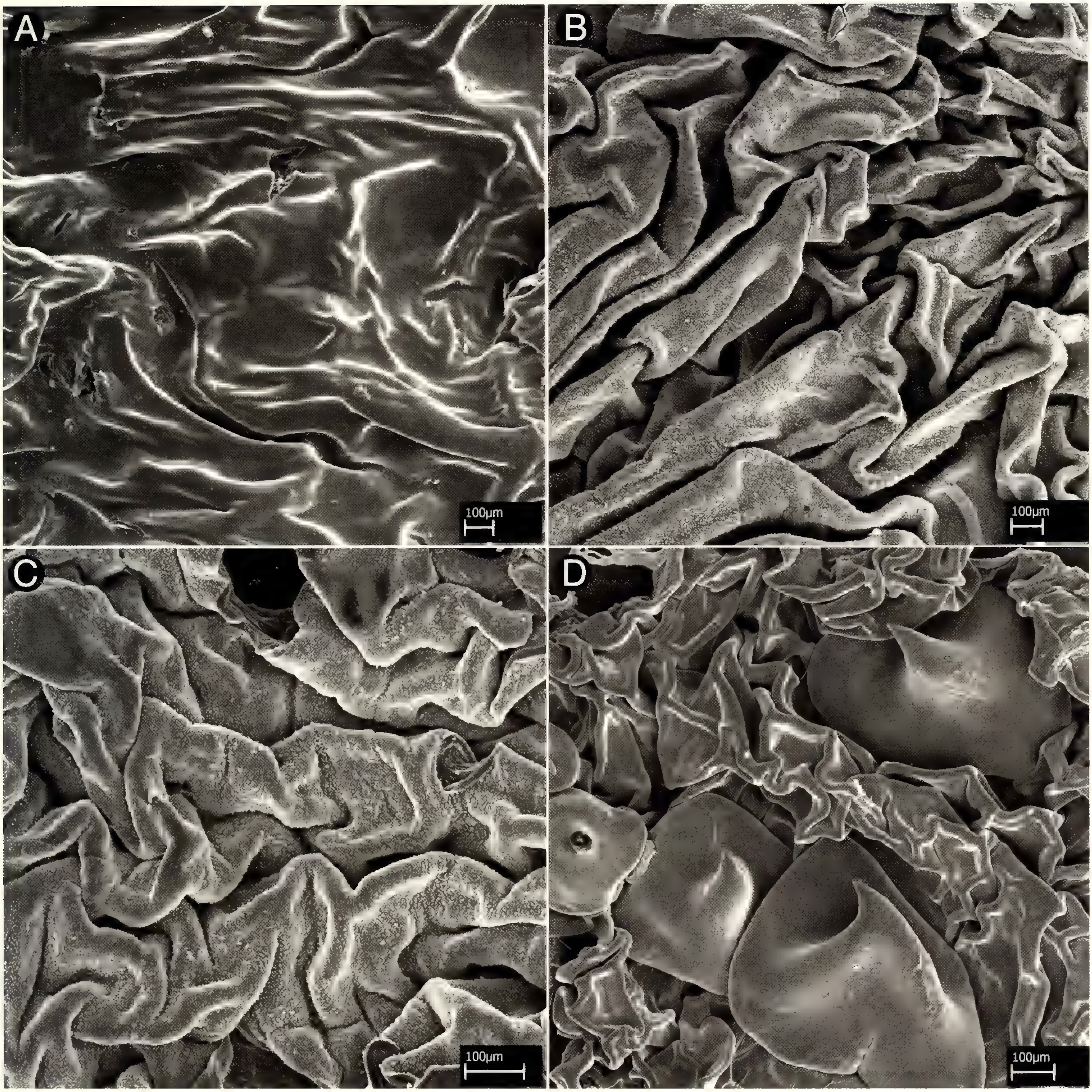
A
100μm
B
100μm
C
100μm
D
100μm

Figure 1. Scanning electron micrographs of the vaginal cuticular lining of (A) *Otinodoris winckworthi*, (B) *Platydoris formosa*, (C) *Platydoris scabra*, and (D) *Platydoris angustipes*.

Vaginal cuticular lining and penial hook interaction

The holes observed in the vaginal cuticular lining of a single specimen of *Otinodoris winckworthy* were most likely the result of interaction with the penis during copulation. The fact that the diameters of the holes were similar to the diameters of the tips of the penial hooks of the same specimen, indicates that they may correspond to the sites where the penial hooks of the partner anchored during copulation. The tips of the penial hooks of that same specimen were separated by a wider distance than the separation between holes. However, the distance between penial hooks in the sample examined did not reflect the actual distance in the living, everted penis, which is dilated as a consequence of perfusion of blood from the hemocoel into the penial tissue (Evans 1914). It is also possible that the copulating partner was smaller in size and therefore had a smaller penis. These would explain the differences in the distances between the holes and the tips of the hooks.

Several cuticular linings of species of the genus *Platydoris* were examined, and in none of them were similar holes found. All of these specimens were preserved in the same conditions and studied with the same methods, therefore the possibility that the holes are an artifact of preservation seems unlikely. Due to the presence of comparatively large pitches (or folded areas) and the rough surface on the vaginal cuticle in *Platydoris* spp., penetration of the vaginal lining is unlikely to be necessary for anchorage; the pitches probably prevent penetration from occurring. The penial hooks could fit among the numerous pitches without damaging the vaginal lining.

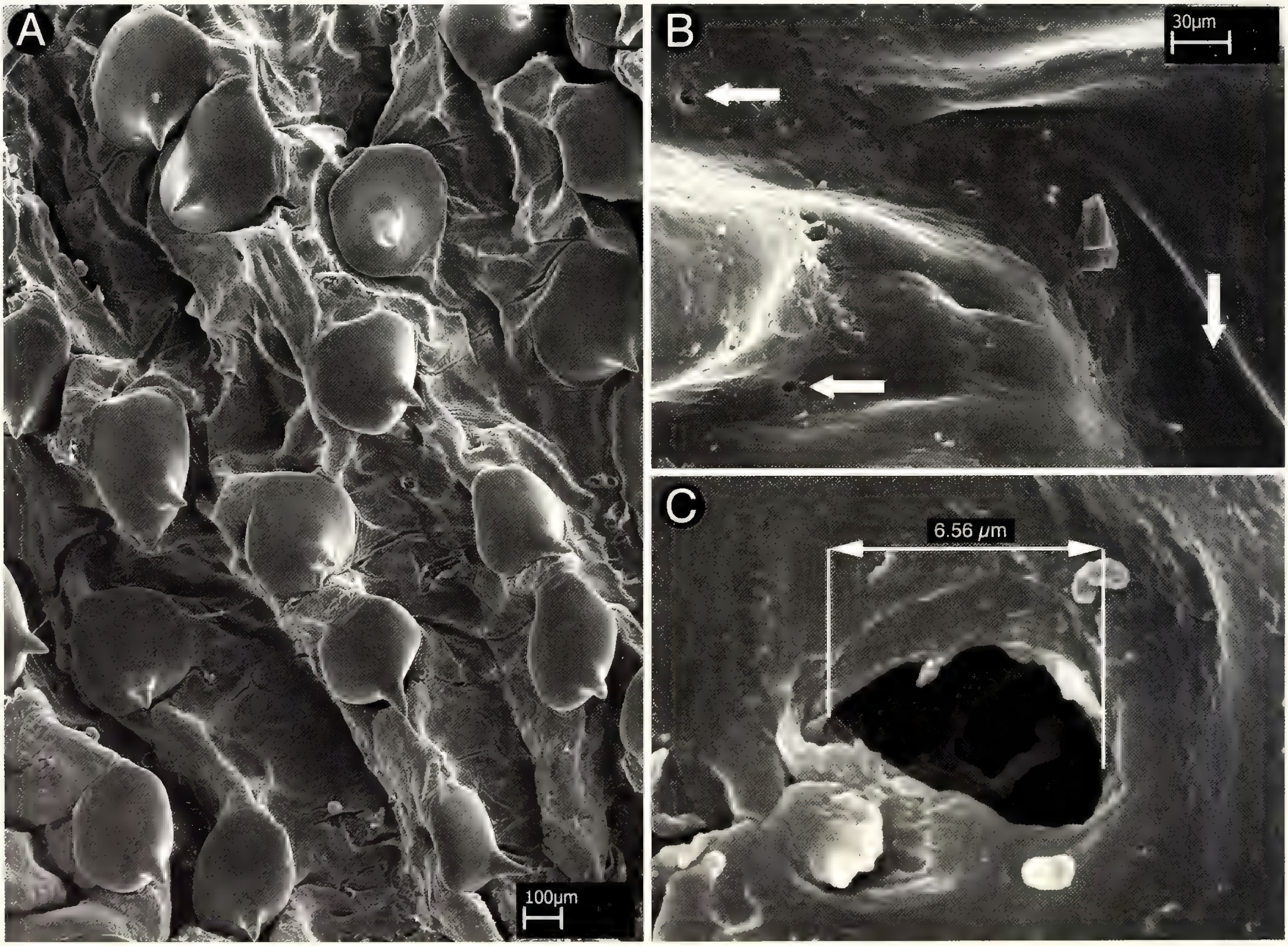

Figure 2. Scanning electron micrographs of the penis and vagina of *Otinodoris winckworthi*. A. Penial hooks. B. Holes on the vaginal cuticular lining. The white arrows indicate the holes. C. Detail of a hole.

Functional adaptations of the vagina

In all species of *Platydoris* examined, the presence of a folded cuticular lining may provide a better anchorage for the penial hooks of the partner during copulation without damaging the vagina. In *Otinodoris winckworthi*, where some damage was observed, the cuticular lining may offer a more stable substrate for the penial hooks, which appear to penetrate the hard surface of the cuticle.

The genera *Otinodoris* and *Platydoris* include species that reach large sizes, considerably larger than most other groups of dorid nudibranchs. The presence of the cuticular lining may provide an advantage for larger individuals, probably related to the forces involved in the potential separation of larger individuals during copulation.

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Growth and gametogenic cycle of the transverse ark, *Anadara transversa* (Say, 1822), in coastal Georgia

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Abstract: The growth rate and reproductive cycle were determined for the transverse ark, *Anadara transversa* held in pearl nets in the Skidaway River, Georgia during 1996 and 1997. The arks grew from an initial mean shell length of 10.3 ± 0.2 mm in June 1996 to 25.2 ± 0.34 mm in September 1997. Growth was well described by the von Bertalanffy growth model: $K = -0.52$, $L_\infty = 24.93$, $t_0 = -0.02$. Arks were noted to reach sexual maturity early, with 80% of individuals ($n = 30$) examined in October 1996 achieving the ripe stage. Some spawning was observed in December 1996 and January 1997; however, major spawning occurred between May 1997 and July 1997. By August 1997, arks were either spent or inactive and all were dead by October 1997. The overall female-to-male sex ratio was 1.00:0.53. When cultured in pearl nets in Georgia, transverse arks are short lived (< two years), grow rapidly, reach sexual maturity at an approximate size of 10 mm, spawn in May-June, are a semelparous species, and obtain a maximum size of approximately 30 mm.

Key words: gametogenesis, sex ratio, spawning

The transverse ark, *Anadara transversa* (Say, 1822), is a small-sized marine bivalve (shell length less than 38 mm) of the family Arcidae that inhabits the estuarine waters of the eastern United States from Cape Cod, Massachusetts through the states bordering the Gulf of Mexico and extends into the West Indies (Abbott 1974). This is a fairly common species, particularly in the northern part of its range, where it lives in mud below the low-water line. *Anadara transversa* has a quadrate-oval shell with a slight overlapping of the left valve over the right. Each valve has 30-35 ribs; those on the left valve are usually beaded. The shell color is white with grayish brown periostracum (Emerson and Jacobson 1976, Abbott 1991). In the Chesapeake Bay, this species inhabits areas where the salinity is above 15 ppt (Castagna and Chanley 1973). Little life-history information exists for this species in the United States. Loosanoff and Davis (1963) and Loosanoff *et al.* (1966) have described larval development and larval size dimensions. Chanley and Andrews (1971) reported a spawning period from May to September in Virginia as evidenced by the presence of larvae in the water column. This study describes the growth and gametogenic cycle of the species for the first time from the coastal waters of Georgia.

METHODOLOGY

Small transverse arks were collected from a shipment of seed of the northern quahog, *Mercenaria mercenaria* (Linné, 1758), purchased from the "East Coast Hard Clam" hatchery on the Indian River, Florida. While the quahog seed was kept in raceways prior to field planting, arks were observed to migrate to the top of the seed mass and occasionally up the sides of the raceway to the water/surface interface. Thus, arks were readily separated from the quahog seed. Two hundred arks were randomly selected and shell length (maximum anterior-posterior measurement) was recorded to the nearest 0.1 mm with Vernier calipers. Arks had an initial mean shell length of 10.3 ± 0.2 (S.E.) mm with a range of 8.1 to 13.4 mm. To determine the growth rate and gametogenic cycle, approximately 750 arks were placed into two 3-mm mesh pearl nets and were suspended off a floating dock (0.5 m depth) in the Skidaway River at the Skidaway Institution of Oceanography, Savannah, Georgia, in June 1996.

Each month from June 1996 to September 1997, thirty arks were randomly collected, measured for shell length, and a mid-lateral gonadal sample (ca. 1 cm^2) was dissected. Notes were also taken on the coloration of the gonads during dissection. Gonadal tissue was fixed in Davidson's solution (Humason 1967), refrigerated for 48 h, washed with 50% ethanol, and stored in 70% ethanol until processing. Tissue samples were dehydrated in a graded alcohol series, cleared in toluene, and embedded in Paraplast®. Paraffin blocks were sectioned (7-8 µm) with a Leica 820 II Microtome. The tissue sections were deparaffinized with toluene, rehydrated to water, and then stained with hematoxylin and counterstained with eosin (Bancroft and Stevens 1982). Prepared gonadal slides were examined with a Zeiss Standard 20 microscope (objective = 20X), sexed, and assigned to a developmental stage as described by Walker and Heffernan (1994) and

Spruck *et al.* (1994). A staging criterion of 0 to 5 was assigned for Early Active (= 3), Late Active (= 4), Ripe (= 5), Partially Spawned (= 2), Spent (= 1), and Inactive (= 0). Monthly gonadal index (G.I.) values were determined for each sex by averaging the number of specimens ascribed to each category score. Sex ratios were tested against a 1:1 ratio with Chi-Square statistics (Elliott, 1977).

Surface water temperature and salinity for the Skidaway River were measured daily (Monday-Friday) from the dock of the Marine Extension Service, adjacent to the grow-out site, at 0800 h from June 1996 to September 1997.

RESULTS

Monthly averages of surface water temperatures and salinity for the Skidaway River are presented in Figure 1. Water temperatures followed the typical annual pattern, ranging from mean highs of 28.8°C and 29.6°C in July 1996 and July 1997, respectively, to a low of 11.7°C in January 1997. Mean salinity increased from 22.8 ppt in July 1996 to 28 ppt in December 1996, then gradually decreased to 17 ppt by March 1997, before rising again to 26 ppt by September 1997.

Arks grew rapidly during the first few months of deployment (Fig. 2), increasing in size from 10.3 mm in June 1996 to 23.1 mm in October 1996 (3.2 mm/month). Growth subsequently slowed down considerably between October 1996 and September 1997 (23.1 mm to 25.2 mm, 0.19 mm/month). A von Bertalanffy growth model (von Bertalanffy 1938) was applied to the mean monthly shell length data (Figure 2) resulting in the following growth parameters: $K = -0.52$, $L_\infty = 24.93$, $t_0 = -0.02$. The largest size obtained by a single specimen was 30.5 mm in shell length. All arks were dead by October 1997.

Of the 429 specimens examined over the sampling period, 49 (11.4%) were sexually indeterminate, 131 (30.5%) were male, and 249 (58.0%) were female. A Chi-Square test was performed and the overall female/male ratio of 1.89 was found to differ significantly from parity ($x^2 = 18.32$; $p < 0.001$). The sex ratio was not constant throughout the study (Fig. 3) ranging from 0.38 in November 1996 to 8.67 in December 1996. The smallest male exhibiting gametogenesis measured 10.0 mm in shell length, while the smallest female was 10.4 mm; both were at the early active stage of gonadal development in June 1996. Histological examination and observations of fresh tissue indicated that all orange-red colored gonads were characteristic of late-active or ripe females and white gonads were characteristic of late-active or ripe males.

Individuals reached sexual maturity rapidly. Although some animals spawned in December 1996 and January 1997, major spawning occurred between April 1997 and July 1997 (Fig. 4). The low gonadal index (G.I.) value of 0.75 for arks in

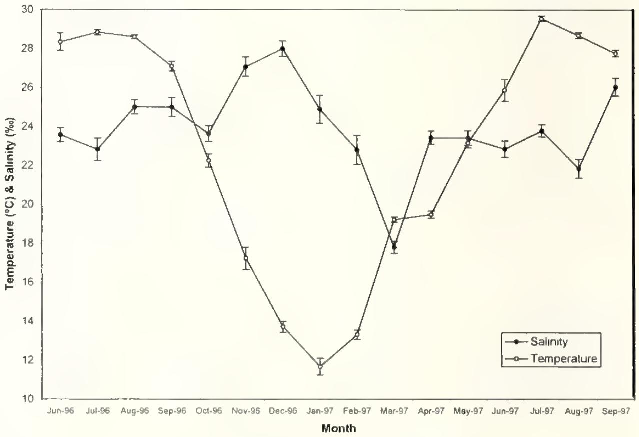

Figure 1. The mean monthly water temperature and salinity of the Skidaway River, Georgia, from June 1996 to October 1997 (vertical bars indicate ± 1 standard error from the mean).

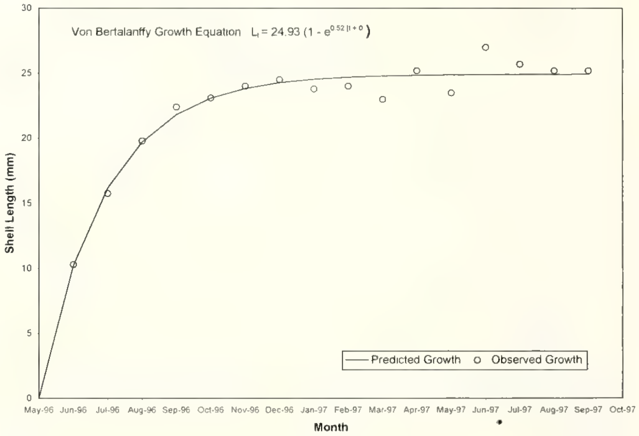

Figure 2. The mean shell length (mm) of transverse arks, *Anadara transversa*, grown in pearl nets suspended in the Skidaway River, Georgia, from June 1996 to October 1997.

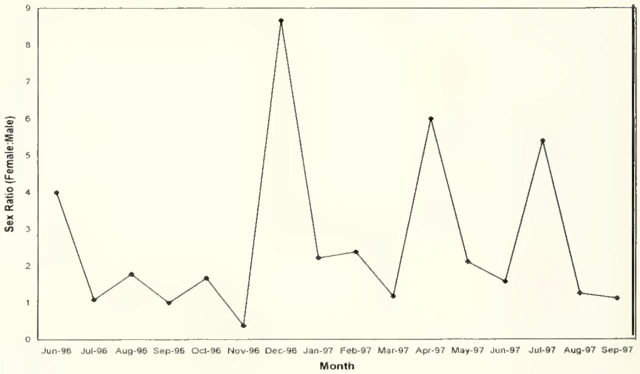

Figure 3. Variations in the female:male ratio of transverse arks, *Anadara transversa* in monthly samples taken from pearl nets suspended in the Skidaway River, Georgia, between June 1996 and October 1997.

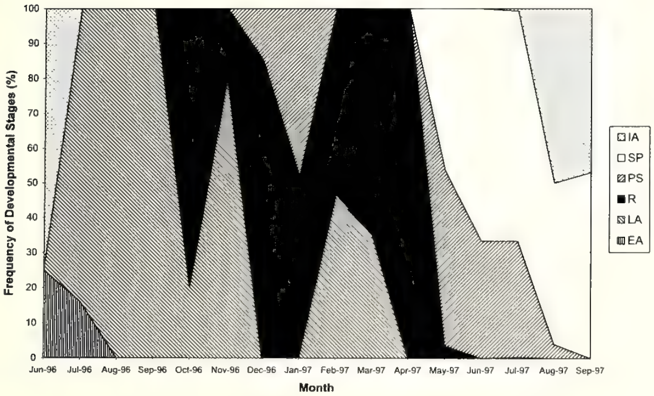

Figure 4. The relative frequency (percentage) of each gonadal developmental phase (IA = inactive, SP = spent, PS = partially spawned, R = ripe, LA = late active, and EA = early active) for the transverse ark, *Anadara transversa*, from June 1996 to October 1997.

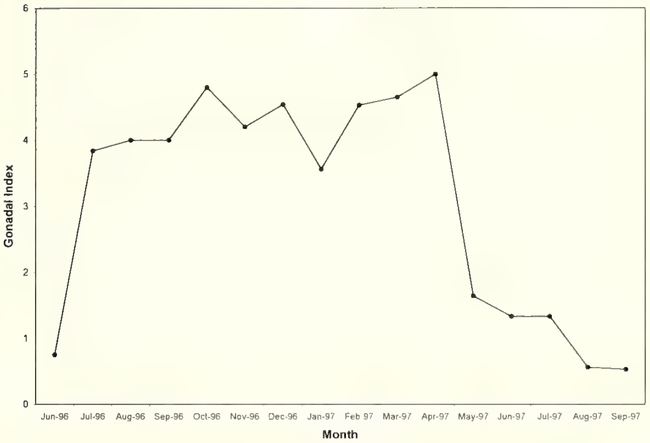

Figure 5. Values of the monthly gonadal index for the transverse ark, *Anadara transversa*, from the coastal waters of Georgia between June 1996 and October 1997. Monthly gonadal index (G.I.) values were determined by averaging the number of specimens ascribed to each category score (inactive = 0, spent = 1, partially spawned = 2, ripe = 5, late active = 4, and early active = 3).

June 1996 (Figure 5) was due to the high number (75%) of inactive individuals (10.1 ± 0.29 mm; range 8.5 mm to 12.9 m) with 25% in the early active stage (11.2 ± 0.45 mm; range 10 mm to 12.5 mm). By July 1996, the G.I. value increased rapidly to 3.84 as all animals were reproductively active and most had entered the late active stage (84%). All were in the late active stages during August and September 1996. The G.I. value increased to 4.8 by October 1996 prior to decreasing to 3.56 by January 1997, reflecting the occurrence of partially spawned individuals in the December (15%) and January (48%) samples. Major spawning commenced after April 1997 when the G.I. reached 5.0 (100% ripe) and lasted from May (50% partially spawned, 46.5% spent, G.I. of 1.64) to July (33% partially spawned, 66% spent, G.I. of 1.33). By August and September 1997 the G.I. decreased to 0.56 and 0.53, respectively, as approximately equal numbers of spent and inactive individuals occurred.

DISCUSSION

Several ark clams form the basis of economically significant molluscan fisheries and extensive culture operations throughout the world (Broom 1985, Manzi and Castagna 1989). Many different species occur in the inshore, nearshore, and offshore waters of the southeastern United States, including *Anadara floridana* (Conrad, 1869), *Arca zebra* (Swainson, 1833), *Noetia ponderosa* (Say, 1822), *Anadara ovalis* (Bruguière, 1789), *Anadara brasiliana* (Lamarck, 1819), and *Anadara notabilis* (Röding, 1798). These species range in shell length from approximately 60 mm to 130 mm. Virginia supports a small-scale ark fishery and there is currently interest in developing an aquaculture-based fishery in Georgia (Power and Walker 2001) and Florida (Leslie Sturmer, Florida Cooperative Extension Service, Cedar Key, pers. comm.). The transverse ark is the smallest ark attaining a maximum reported shell length of 38 mm (30.5 mm in the present study), and does not therefore represent a potential commercial resource. However, very little life information exists for all ark species in the United States. Therefore, when transverse arks recruited into our quahog seed we took the opportunity to examine growth and reproduction in this poorly known species.

The May-July spawning period identified by the present study is consistent with the occurrence and collection of ark spatfall from the quahog seed obtained from the hatchery nursery in the Indian River, Florida, the previous June. There are no other systematic reports on the gametogenic cycle of the transverse ark; however, ark larvae were reported in the water column from Virginia between May and September (Chanley and Andrews 1971). Loosanoff and Davis (1963) collected arks from Long Island Sound in mid May and spawned them within 2 to 3 h. The released eggs were pinkish-orange, as were the eggs found in the present study. Loosanoff and Davis (1963) also reported the presence of pediveligers from June to August with post-larval arks occurring from July to September. From these studies, it would appear that the transverse ark has a similar reproductive pattern in Florida, Georgia, Virginia, and New York.

Temperature is one of the main exogenous factors controlling reproduction in marine invertebrates. Although water temperatures are expected to differ substantially between states across the range of *Anadara transversa*, it should be noted that temperatures in late spring and early summer at each location are warming up considerably. Arks spawned in Georgia as temperatures increased from 19°C in April to 23°C in May (Figure 1), and all spawning was completed by August, when temperatures averaged 29°C. Broom (1983) hypothesized that salinity controlled spawning in the related *Anadara granosa* (Linné, 1758), proposing that a salinity depression that occurs off the west coast of Malaysia with the onset of the intermonsoonal rains may trigger spawning. Similarly, the salinity of the Skidaway River dropped steadily from 28 ppt in December 1996 to 17.80 ppt in March 1997 prior to the onset of major spawning. Thus the initiation of major spawning in transverse arks in the present study may have resulted from changes in both temperature and salinity.

Members of the Arcidae are reported to initiate gametogenesis and reach sexual maturity at a small size (Table 1). Gametogenesis commenced in the transverse ark at approximately 10 mm (shell length) and all arks were ripe at a size of

Table 1. Size at initial gametogenesis and sexual maturity for various marine bivalves species from the Family Arcidae.

Species	**Gender & shell length at initial gametogenesis (mm)**			**Shell length (mm) at sexual maturity of each gender**			**Source**
	Male	**Female**	**Not Stated**	**Male**	**Female**	**Not Stated**	
Anadara cornea						•20	Broom, 1985
Anadara granosa						21	Narasimham, 1968
Anadara granosa			17.5			24-25	Broom, 1983
Anadara ovalis				9.9	11.5		Power and Walker, 2002
Anadara rhombea	19	22		21-25	21-25		Natarajan and John, 1983
Anadara scapha			22			30	Baron, 1992
Anadara senilis	5-9	19	10-17				Yoloye, 1974
Anadara subcrenata			15				Ting *et al.*, 1972
Anadara transversa	4	7		10	12		This study
Anadara tuberculosa				32	36		Broom, 1985

Table 2. The sex ratios and percentage hermaphroditism of various marine bivalves species from the Family Arcidae.

Species	**Sample Size (N)**	**Sexual Ratio (Female:Male)**	**% Hermaphroditism**	**Source**
Anadara antiquata	1040	1.00:1.00		Toral-Barza and Gomez, 1985
Anadara granosa	300	1.00:1.00	0.003	Broom, 1983
Anadara ovalis	185	1.00:1.98		McGraw *et al.*, 1998
Anadara ovalis	747	1.00:2.48	0	Power and Walker, 2002
Anadara rhombea	1155	1.00:1.27	0	Natarajan and John, 1983
Anadara scapha	235	1.00:1.47		Baron, 1992
Anadara senilis	100	1.00:0.34	0	Yoloye, 1974
Anadara senilis		1.00:1.00	0.004	Broom, 1985
Anadara subcrenata		1.00:1.00		Broom, 1985
Anadara transversa	199	1.00:0.53		This study
Anadara trapezia		1.00:1.00		Broom, 1985
Anadara tuberculosa	218	1.00:1.25		Cárdenas and Aranda, 2000
Anadara tuberculosa	1094	1.00:1.00		Cruz, 1984
Anadara tuberculosa		1.00:1.00		Dzyuba and Maslennikova, 1982
Noetia ponderosa	181	1.00:1.26		McGraw *et al.*, 1998

24 mm. A rapid growth rate during year one and a small size at sexual maturity have been previously documented for other species of ark, although the commercial species listed in Table 1 achieve a much larger overall size and live longer than does the transverse ark. Females dominated the population of the transverse ark in Georgia, which is not in general agreement with previous findings for other ark species. A dominance of females is only reported in one other ark species, *Anadara senilis* (Yoloye 1974); Broom (1985) observed an equal sex ratio in the same species. Incidence of hermaphroditism in arks is apparently rare (Table 2), and was not observed in the present study.

Qualitative histological data and quantitative growth data indicate that *Anadara transversa* when cultured in pearl nets in Georgia is a short-lived species (less than two years) that grows and matures rapidly, has a high female to male ratio, has one major spawning event in the late-spring, early-summer months and then dies in the fall. Thus it can be viewed as a semelparous species.

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Changes in the freshwater mussel (Bivalvia: Unionidae) fauna of the Bear Creek system of Northwest Alabama and Northeast Mississippi

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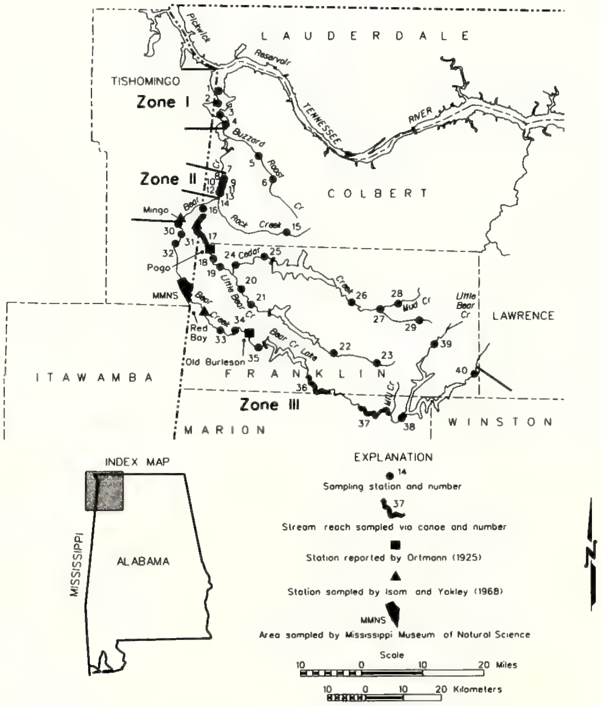
Abstract: Drastic reductions in diversity and abundance of mussel populations are documented in many systems. Bear Creek, located in northwest Alabama and northeast Mississippi, has seen changes to its fauna, possibly the result of impoundment, channelization, wastewater discharge, and sedimentation from such sources such as strip mining, agriculture, and silviculture. The most obvious influences have been impoundment of the lowermost 32 km of Bear Creek by Pickwick Reservoir of Tennessee River, the construction of four dams within the system, construction of a 29-km-long channel designed to limit flooding, and bank destabilization. Mussels are absent from much of the system and faunal composition has apparently been altered where mussels persist, based on comparison to limited previous studies. The most notable changes are the loss of Cumberlandian species diversity and the apparent increase in Ohioan species diversity. We sampled 40 stations in the Bear Creek system and report 32 mussel species live or fresh dead, including 3 Cumberlandian species, and 2 others weathered dead. Fourteen of these species were not reported in two earlier studies. During this study the most depauperate populations were upstream of Bear Creek km 41.0 and in tributaries. No mussels were collected immediately downstream of dams, and diversity gradually increased downstream from the lowermost main channel dam until 28 species occurred together in a free-flowing reach shortly before entering Pickwick Reservoir. One weathered dead zebra mussel, *Dreisenna polymorpha*, was also collected, representing a new tributary record. The population of *Epioblasma brevidens* in Bear Creek is the only population of that species known in the lower Tennessee River system, and the population of *Lexingtonia dolabelloides*, another new tributary record, is one of only two populations of that species known downstream of Paint Rock River.

Key words: perturbations, natural systems, diversity, abundance

Changes to mussel faunas, brought about by human perturbations to natural systems during the past two hundred years, have been extreme through most of North America. Drastic reductions in diversity and abundance have been well documented in many systems (*e.g.* Stansbery 1961, 1973, Athearn 1967, Stein 1972, Hurd 1974, Parmalee *et al.* 1982, Ahlstedt 1983, Houp 1993, McGregor *et al.* 2001, Garner and McGregor 2001). Bear Creek, located in northwest Alabama and northeast Mississippi (Fig. 1), has been the recipient of human induced damage in the form of impoundment, channelization, waste water discharge, and sedimentation from such sources as strip mining and agricultural and silvicultural practices.

The lowermost 32 km of Bear Creek have been impounded as part of Pickwick Reservoir of Tennessee River since 1938. Four flood-control dams were completed within the Bear Creek system between 1969 and 1979. Two of these dams were on the main channel, at Bear Creek km (BCK) 120 (1969) and BCK 184 (1978), and one each on Little Bear Creek at km 18.5 (1975), and Cedar Creek at km 37.5 (1979) (Tyler Baker and Berry Stalcup, Tennessee Valley Authority, pers. comm.). Other human alterations to habitat associated with flood control include channelization of selected reaches and a 29-km-long floodway built to limit flooding during high water events (Taylor and Hall 1974). Before construction of the dams and channelization, Bear Creek supported a benthic fauna representative of a moderately diverse and stable community, characteristic of the low gradient streams in this geographical area (Taylor and Hall 1974). In the early 1990s Bear Creek was rated poor for fish and benthic life and was reported to suffer from streambank erosion (Tennessee Valley Authority 1994). Bear Creek Lake rated poor in dissolved oxygen (DO) content and fair in all other categories evaluated, with an overall poor rating. Little Bear Creek Lake also rated poor in DO content, but fair overall. Cedar Creek Lake received ratings of good to poor. During warmer months water is retained in Upper Bear Creek Lake on weekdays and controlled surface releases on weekends provide sustained flow for recreational canoeing downstream.

The focus of this study was to document the current mussel fauna of the system, with emphasis on the spatial relationships between species richness and human alterations to the system. General comparisons were made with two earlier studies.


L A U D E R D A L E
Pickwick
Reservoir
TENNESSEE
RIVER
TISHOMINGO
Zone I
Buzzard
Roost
Cr
Zone II
COLBERT
Mingo
Bear
Rock
Creek
Pogo
Cedar
Creek
Little
Bear
Cr
Mud
Cr
Little
Bear
Cr
LAWRENCE
MMNS
Bear
Creek
Red
Bay
Old Burleson
Bear Cr Lake
I T A W A M B A
F R A N K L I N
Zone III
Mill Cr
M A R I O N
W I N S T O N
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
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21
22
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39
40
INDEX MAP
MISSISSIPPI
ALABAMA
EXPLANATION
14
Sampling station and number
37
Stream reach sampled via canoe and number
Station reported by Ortmann (1925)
Station sampled by Isom and Yokley (1968)
MMNS
Area sampled by Mississippi Museum of Natural Science
Scale
10 0 10 20 Miles
10 0 10 20 Kilometers
N

Figure 1. Location of study area showing sampling stations and zones, political boundaries, and nearby landmarks.

STUDY AREA

Bear Creek (Fig. 1) is a 217 km-long southern tributary of Tennessee River. The system drains 2,450 km^2 in Colbert, Franklin, Lawrence, and Winston counties, Alabama, and Itawamba and Tishomingo counties, Mississippi, with about 85% of the watershed in Alabama (Mettee *et al.* 1996). In the early 1970s, approximately 70% of the watershed was forested, 20% was in miscellaneous use, such as commercial enterprise, roads, towns, *etc.*, and 10% was in agricultural use (Taylor and Hall 1974). In 1990, over 75% of the watershed was forested (U.S. Environmental Protection Agency 1990). Elevations range from 335 m above mean sea level (msl) in the headwaters to 126 m above msl at its confluence with the Tennessee River (Hollingsworth 1991).

Isom and Yokley (1968) discussed the areal geology in detail. Bear Creek originates in the Warrior Basin of the Cumberland Plateau, with some of the eastern tributaries originating in the Moulton Valley of the Highland Rim. The middle reaches of the system lie within the Fall Line Hills of the East Gulf Coastal Plain and the lower 25.7 km of Bear Creek flow through the Tennessee Valley of the Highland Rim (Isom and Yokley 1968, Sapp and Emplaincourt 1975). During this survey, stations in unimpounded stream reaches were of alternating shoal/pool character. Substrata of shoals were clean-swept gravel and substrata in pools were silty gravel and/or sand. At impounded stations, substrata were varying combinations of silt, sand, and gravel.

METHODS

This study included a system-wide, qualitative survey of 40 sampling stations in Bear Creek and six tributaries: Buzzard Roost, Cedar, Little Bear (tributary to Bear Creek), Little Bear (tributary to Cedar Creek), Mud, and Rock creeks (Fig. 1, Table 1). We sampled for mussels using glass-bottomed viewing buckets and mask and snorkel in shallow water. Sampling was limited to summer months (June-September) in 1995, 96, 97, and 99, and in May 2000. Some records were secured when shells were encountered during unrelated studies. The lower 11 km of Bear Creek were sampled from a dive boat equipped with surface air supply and by wading and hand picking along some shorelines and mud flats during low water periods. Shoreline and mud flat sampling stations are not depicted in Figure 1 or listed in Table 1. At each station all habitat types were sampled and effort continued until workers were satisfied that most or all species present had been recorded. The duration of each sampling trip was two to four person hours, except while diving (bottom time ranged from 15-45 minutes). In most cases, live animals were identified in the field and released. Most fresh dead shell material was retained with voucher specimens deposited in the Ohio State University Museum of Biological Diversity (OSUM) and Mississippi Museum of Natural Science (MMNS). Nomenclature follows Turgeon *et al.* (1998). Different reaches of the main channel of Bear Creek where mussel collections were made are grouped into zones. Zone I represents the impounded lower portion of Bear Creek, Zone II represents the lower free flowing reach of stream with relatively intact mussel habitat, and Zone III the upper reach of the creek where habitat has been more severely altered.

RESULTS

We encountered 32 live or fresh dead mussel species. Two species, *Pleurobema oviforme* (Conrad, 1834) and *Strophitus undulatus* (Say, 1817), were represented by weathered dead shells only (*i.e.* nacre of shells somewhat chalky) (Table 2). Live or fresh dead Asian clams, *Corbicula fluminea* (Müller, 1774), were collected at many stations in the main channel and tributaries, and were absent only in small tributaries and headwater reaches. This species will not be discussed in detail and is not included in station totals or abundance and diversity accounts.

Table 1. Mussel sampling stations in the Bear Creek system, Alabama and Mississippi, 1996-2001. All localities are in Alabama except Tishomingo County, Mississippi.

Station no.	Locality	Coordinates
1	Bear Creek opposite Colbert Park, BCK 5.3, Colbert County	T. 2 S., R. 15 W., sec. 34
2	Bear Creek off point on left bank, BCK 6.8, Colbert County	T. 3 S., R. 15 W., sec. 3
3	Bear Creek near Cary Hollow, BCK 8.5, Colbert County	T. 3 S., R. 15 W., sec. 3
4	Bear Creek off point at BCK 11.3, Colbert County	T. 3 S., R. 15 W., sec. 15
5	Buzzard Roost Creek at Highway 4, Colbert County	T. 4 S., R. 14 W., sec. 4
6	Buzzard Roost Creek at Highway 21, Colbert County	T. 4 S., R. 14 W., sec. 22
7	Bear Creek, upstream of Highway 4, BCK 32.2, Colbert County	T. 4 S., R. 15 W., sec. 23
8	Bear Creek at Harris Hollow, BCK 34.3, Colbert County	T. 4 S., R. 15 W., sec. 22
9	Bear Creek below Wills Creek, BCK 36.5, Colbert County	T. 4 S., R. 15 W., sec. 26
10	Bear Creek at Wills Creek mouth, BCK 37.3, Colbert County	T. 4 S., R. 15 W., sec. 26
11	Bear Creek above Wills Creek, BCK 38.0, Colbert County	T. 4 S., R. 15 W., sec. 27/34
12	Bear Creek near Johnson Branch, BCK 39.2, Colbert County	T. 4 S., R. 15 W., sec. 34
13	Bear Creek at Natchez Trace, BCK 39.5, Colbert County	T. 4 S., R. 15 W., sec. 34
14	Bear Creek at Rock Creek mouth, BCK 41.0, Colbert County	T. 5 S., R. 15 W., sec. 3
15	Rock Creek at Highway 21, Colbert County	T. 5 S., R. 14 W., sec. 26
16	Cedar Creek near Natchez Trace, Colbert County	T. 5 S., R. 15 W., sec. 8
17	Cedar Creek near Natchez Trace, Tishomingo County	T. 5 S., R. 11 E., sec. 21*
18	Cedar Creek near Pogo, Franklin County	T. 6 S., R. 15 W., sec. 10
19	Cedar Creek at Highway 15, Franklin County	T. 6 S., R. 15 W., sec. 10
20	Little Bear Creek at Alabama Highway 247, Franklin County	T. 6 S., R. 14 W., sec. 32
21	Little Bear Creek at Alabama Highway 24, Franklin County	T. 7 S., R. 14 W., sec. 15
22	Little Bear Creek at Alabama Highway 187, Franklin County	T. 7 S., R. 13 W., sec. 35
23	Little Bear Creek at County Highway 59, Franklin County	T. 8 S. R. 12 W., sec. 11
24	Cedar Creek at Highway 23/90, Franklin County	T. 6 S., R. 15 W. sec. 13
25	Cedar Creek at Alabama Highway 247, Franklin County	T. 6 S., R. 14 W., sec. 10/11
26	Cedar Creek near Alabama Highway 247, Franklin County	T. 6 S., R. 12 W., sec. 32
27	Cedar Creek at U.S. Highway 43, Franklin County	T. 7 S., R. 12 W., sec. 12
28	Mud Creek at Highway 99 bridge, Franklin County	T. 7 S., R. 11 W., sec. 7
29	Cedar Creek at Highway 75/74, Franklin County	T. 7 S., R. 11 W., sec. 14
30	Bear Creek at Highway 30, BCK 50.0, Tishomingo County	T. 5 S., R. 11 E., sec. 21
31	Bear Creek at Tishomingo Park, BCK 55.5, Tishomingo County	T. 5 S., R. 10 E, sec. 25
32	Bear Creek at Highway 86, BCK 62.8, Tishomingo County	T. 6 S., R. 11 E., sec. 7
33	Bear Creek at Highway 25, BCK 109.4, Franklin County	T. 7 S., R. 14 W., sec. 30
34	Bear Creek at Highway 4, BCK 115.5, Franklin County	T. 7 S., R. 14 W., sec. 33
35	Bear Creek at Highway 37, BCK 120.4, Franklin County	T. 8 S., R. 14 W., sec. 2
36	Bear Creek from Highway 57 to Highway 187, Franklin County	T. 8 S., R. 13 W., sec. 27*
37	Bear Creek from Mill Creek to Highway 172, Marion County	T. 9 S., R. 11 W., sec. 13*
38	Bear Creek at Alabama Highway 13, Marion County	T. 9 S., R. 11 W., sec. 10
39	Little Bear Creek at County Highway 34, Franklin County	T. 7 S., R. 10 W., sec. 31
40	Bear Creek at County Hwy. 93, Franklin County	T. 8 S., R. 10 W., sec. 24

* Coordinates for stream reaches sampled via canoe are approximately mid-reach.

Table 2. Comparison of collection records among stations in the Bear Creek system, 1996-2001.

Species	**Stations** 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Amblema plicata		x					x		x	x	x	x	x	x		w	w	x	x		
Anodonta suborbiculata	x		x																		
Arcidens confragosus		w		w										x							
Cyclonaias tuberculata							w		x	w	x	x	x	x					x		
Elliptio crassidens							x	w	x	x	x	x	x	x		w					
Ellipsaria lineolata									w		x	x	x	x							
Epioblasma brevidens											x		x	x							
Fusconaia ebena											x	x	x	x							
Lampsilis abrupta												x									
L. fasciola														x							
L. ovata							x			x	x	x	x	x		w					
Lasmigona c. complanata										x	x		x	x							
L. costata							w						x	x							
Leptodea fragilis		w					x	w	w	x	x	x	x	x		x	w		x		
Lexingtonia dolabelloides										x	x	x	x	x							
Ligumia recta												x		x							
Megalonaias nervosa							x	w	x	x	x	x	x	x			w				
Obliquaria reflexa		x					x			x	x	x	x	x							
Pleurobema oviforme																					
Potamilus alatus		x					x	w	x	x	x	x	x	x		x	w	x			
P. ohiensis[1]																					
Ptychobranchus fasciolaris									x	w		x	w	x							
Pyganodon grandis		x												w							
Quadrula apiculata													x								
Q. cylindrica													x	x							
Q. pustulosa		x					x		w	x	x	x	x	x		x	w		w		
Q. quadrula		x	x	x			x	x	x	x	x	w	x	x			w				
Strophitus undulatus																					
Toxolasma parvus[1]																					
Tritogonia verrucosa											x			x			w				
Truncilla donaciformis											x		w	x							
T. truncata											x		x	x							
Utterbackia imbecillis		x									x				w						
Villosa vanuxemensis vanuxemensis					x																
Dreissena polymorpha[2]																					
Totals	1	9	2	2	1	0	11	5	10	13	19	16	21	25	1	6	7	3	4	0	0

Twelve mussel species were collected from Stations 1-4 (BCK 5.3-11.0) in the lower end of the impounded reach of Bear Creek (Table 2; Fig. 1, Zone I). Ten species were collected while diving and two additional species while hand picking along the shoreline during periods of low water. Diversity averaged 2.8 species/station at four stations sampled by diving in this area. Three species, *Anodonta suborbiculata* Say, 1831, *Potamilus ohiensis* (Rafinesque, 1820), and *Toxolasma parvus* (Barnes, 1823), collected here did not occur in the free flowing reaches. The first record of the exotic zebra mussel, *Dreissena polymorpha* (Pallas, 1774) in Bear Creek was documented when a single weathered dead shell was found cast up on the shore at about BCK 1.6.

Table 2. (continued)

Species	**Stations**																		
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Amblema plicata			w			x	w		w			w							
Anodonta suborbiculata																			
Arcidens confragosus																			
Cyclonaias tuberculata									w										
Elliptio crassidens									w										
Ellipsaria lineolata									w							w			
Epioblasma brevidens																			
Fusconaia ebena																			
Lampsilis abrupta																			
L. fasciola																			
L. ovata			w												x	x			
Lasmigona c. complanata																			
L. costata																			
Leptodea fragilis									w	w									
Lexingtonia dolabelloides																			
Ligumia recta									w										
Megalonaias nervosa									x										
Obliquaria reflexa									x										
Pleurobema oviforme						w													
Potamilus alatus				x					x				x		w				
P. ohiensis[1]																			
Ptychobranchus fasciolaris									w										
Pyganodon grandis					x	w	x		w										
Quadrula apiculata																			
Q. cylindrica																			
Q. pustulosa									x			w			w				
Q. quadrula			x																
Strophitus undulatus									w										
Toxolasma parvus[1]																			
Tritogonia verrucosa			w		w							x			w	x			
Truncilla donaciformis																			
T. truncata												x							
Utterbackia imbecillis													x						
Villosa vanuxemensis vanuxemensis																			
Dreissena polymorpha[2]																			
Totals	0	0	4	1	2	3	2	0	13	1	0	4	2	0	4	3	0	0	0

[1] Fresh dead shells found cast up on shore in impounded lower Bear Creek reach; not included in any station total.

[2] Weathered dead shell found cast up on shore in impounded lower Bear Creek reach; not included in any station total.

x—Denotes live or fresh dead animals collected.

w—Denotes only weathered dead shells collected.

Table 3. Results of mussel surveys in the Bear Creek system. Nomenclature follows Turgeon *et al.* (1998) and designation of Cumberlandian and Ohioan species follows Ortmann (1925), van der Schalie (1939), and Stansbery (1964).

Species	**Ortmann, 1925**	**Isom and Yokley, 1968**	**Present study, 1996-2001**
Cumberlandian			
Actinonaias pectorosa	X		
Epioblasma brevidens		X	X
Epioblasma capsaeformis	X		
Epioblasma turgidula	X		
Fusconaia barnesiana	X	X	
Fusconaia cuneolus	X		
Lampsilis virescens	X		
Lexingtonia dolabelloides			X
Pleurobema oviforme	X		X
Toxolasma lividus	X		
Villosa iris [1]	X		
Villosa v. vanuxemensis	X		X
Ohioan			
Amblema plicata	X	X	X
Anodonta suborbiculata			X
Cyclonaias tuberculata			X
Ellipsaria lineolata		X	X
Elliptio crassidens		X	X
Fusconaia ebena			X
Lampsilis abrupta			X
Lasmigona c. complanata			X
Ligumia recta		X	X
Megalonaias nervosa		X	X
Obliquaria reflexa		X	X
Obovaria subrotunda	X		
Potamilus alatus		X	X
Potamilus ohiensis			X
Pyganodon grandis			X
Quadrula pustulosa	X	X	X
Quadrula quadrula			X
Tritogonia verrucosa	X	X	X
Truncilla donaciformis		X	X
Truncilla truncata	X	X	X
Utterbackia imbecillis			X
Unknown			
Alasmidonta marginata	X		
Arcidens confragosus			X
Epioblasma triquetra	X		
Lampsilis fasciola	X	X	X
Lampsilis ovata [2]	X	X	X
Lasmigona costata	X		X
Leptodea fragilis		X	X
Ptychobranchus fasciolaris	X		X
Quadrula apiculata			X
Quadrula c. cylindrica	X	X	X
Strophitus undulatus			X
Toxolasma parvus			X
Total	22	17	34

[1] Reported by Ortmann as *Villosa nebulosa*; see Parmalee and Bogan (1998) for discussion of *Villosa iris* taxonomy.

[2] Reported by Ortmann as *Lampsilis ovata ventricosa*.

Twenty-seven species were collected live or fresh dead from Station 7, located just upstream of the impoundment of Pickwick Reservoir (BCK 35.4) to Station 14 (BCK 41.0) (Table 2; Fig. 1, Zone II). Included were two Cumberlandian species, *Epioblasma brevidens* (Lea, 1831) and *Lexingtonia dolabelloides* (Lea, 1840). Diversity of live or fresh dead species averaged 13.1 species/station. This reach yielded the only federally listed endangered species of the survey, *E. brevidens* and *Lampsilis abrupta* (Say, 1831). The collection of *L. dolabelloides* represents a new tributary record.

Few mussels were found in the main channel of Bear Creek upstream of Station 14 (Fig. 1, Zone III) or in tributaries (Table 2). Fourteen of 28 stations sampled in those reaches yielded no live or fresh dead mussels. Thirteen species were found live or fresh dead at the remaining 14 stations, averaging 1.9 species/station. Only three species were found in these reaches that were not also found in the main channel of Bear Creek from Zone II. These include *Strophitus undulatus* (one weathered dead shell from Station 30), *Villosa vanuxemensis vanuxemensis* (Lea, 1838) (one fresh dead shell from Station 5) and *Pleurobema oviforme* (one weathered dead shell from Station 27). However, MMNS personnel collected 28 species (seven live) at several sampling stations in Mississippi near the Alabama state line in recent years, suggesting that at least pockets of unioninds are scattered upstream of Station 14. There, *Epioblasma brevidens* and *Lexingtonia dolabelloides* were among the species collected dead, but no information on conditions of dead species were reported and it is unclear if these populations persist (Robert Jones, MMNS, pers. comm.).

DISCUSSION

Bear Creek lies in an interesting zone of mixing for two of the most diverse mussel faunas in the world, the Cumberlandian and Ohioan, but there were no adequate surveys of the system historically. However, brief glimpses of the historic fauna by Ortmann (1925) and Isom and Yokley (1968) give at least some insight into earlier assemblages. This survey provided information on current status of the mussel fauna in the Bear Creek system and allowed for plausible, if somewhat speculative, intimation of temporal changes within the system. Two changes noted during this survey were apparent decimation of the mussel fauna through much of the drainage and loss of Cumberlandian elements with apparent colonization by Ohioan species.

In this study, the most depauperate mussel populations were found upstream of BCK 41.0 (Station 14) and in tributaries (Stations 15-40). Though no historic information exists for most of those areas, they likely held mussel populations similar to those reported by Ortmann (1925) historically. If that is the case, the main channel fauna upstream of Station 14 has been decimated. The loss of diversity in those reaches appears to be the result of habitat destruction, diminished water quality and altered flow regimes. Many of the deleterious effects resulted from impoundment of some reaches of the system, compounded by channelization and poor agricultural and silvicultural practices. Isom and Yokley (1968) reported "pristine" conditions in 1965, just prior to construction of the dams. During this study, we found few or no mussels (none live) immediately downstream of impoundments (Stations 21, 25, 35, and 38). At those stations the creeks were usually channelized, banks were stabilized with riprap, and little canopy cover was present. Though no water quality variables were measured during this study, water just downstream of dams was generally warm, with an unpleasant odor. Heavy growths of algae were observed on the substrata. A few pulmonate gastropods (Lymnaeidae) were collected from stream margins immediately downstream of the impoundments and a few dead *Corbicula fluminea* shells were encountered.

Water quality apparently improves gradually downstream of Bear Creek Dam (BCK 184), enough to support a healthy mussel community just before entering the Pickwick impoundment. Partial recovery is achieved 11 km downstream of the dam (station 33) where four species were collected (two live or fresh dead and two weathered dead). Personnel of MMNS collected seven species live and 21 dead at several stations beginning 34 km downstream of the dam. The most diverse mussel community in the system was found between BCK 35.4 and BCK 41.0 (Fig. 1, Zone II, Stations 7-14, inclusive), where 27 species were collected, with recruitment noted for several species (Table 2). Vaughn and Taylor (1999) reported a strong, gradual, linear increase in mussel species richness and abundance with downstream progression from several impoundments on Little River, Oklahoma. They attributed this phenomenon to the recovery of temperature and flow regimes. There, recovery of the mussel fauna began about 20 km downstream and reached full recovery about 53 km downstream of impoundments. Cedar Creek enters Bear Creek 44.6 km downstream of Bear Creek Dam and its discharge may increase flow to a volume or level of quality suitable for more successful mussel habitation or habitation by potential host fishes. Further evidence of this recovery gradient is supported by results of a recent, unrelated study that showed diversity of fish communities increase with downstream progression from reservoirs in the Bear Creek system (Phillips 2001).

Compositional changes in the mussel fauna of the Bear Creek system have not been uniform between the Cumberlandian and Ohioan groups, with loss of most

Cumberlandian elements and possible gain of Ohioan elements. The Cumberlandian fauna is comprised of species originating in the upper Tennessee and Cumberland river systems (Ortmann 1924, 1925). The Ohioan fauna consists of species thought to have originated in the lower Ohio River and its vicinity (Ortmann 1925). Many Cumberlandian species have proven to be highly intolerant of modern habitat degradation and are now imperiled or extinct.

Ortmann (1925) reported 22 species in collections from two stations made by H.H. Smith in 1910. They included seven Cumberlandian species representing 32% of the total, and five Ohioan species representing 23% of the total (Table 3). The remaining 10 species were of unknown origin. Loss of Cumberlandian elements from the fauna appears to have been underway when Isom and Yokley (1968) visited the system, though their work was prior to construction of the first dam in the drainage. They encountered 17 species on single visits to three stations in 1965 and reported only two Cumberlandian species, which comprised 12% of the total. They reported only eight species that were also reported by Ortmann (1925). The present survey was much more extensive and intensive than either previous study and produced 32 species live or fresh dead, including three Cumberlandian comprising 9% of the total (excluding *Pleurobema oviforme* which was found as weathered dead shell only) (Table 3). Fourteen species are reported from the Bear Creek system for the first time here, bringing the cumulative total of species known from the system to 45.

Disparity among earlier surveys and this one are almost certainly due in part to sampling effort. We made a total of 13 visits to stations in Zone II between August 1997 and July 2000. Neither of the previous studies offered information on sampling techniques, and sampling efficiency is unknown as well. However, loss of Cumberlandian elements is obvious and there may be a trend toward increasing proportion of Ohioan species. Seven of the species reported from Bear Creek for the first time by Isom and Yokley (1968), *Ellipsaria lineolata* (Rafinesque, 1820), *Elliptio crassidens* (Lamarck, 1819), *Ligumia recta* (Lamarck, 1819), *Megalonaias nervosa* (Rafinesque, 1820), *Obliquaria reflexa* Rafinesque, 1820, *Potamilus alatus* (Say, 1817), and *Truncilla donaciformis* (Lea, 1828), belong to the Ohioan fauna (Ortmann 1925, van der Schalie 1939, Stansbery 1964) (Table 3). The other two species first reported from the system by Isom and Yokley (1968) were *Epioblasma brevidens*, of Cumberlandian origin, and *Leptodea fragilis* (Rafinesque, 1820), of unknown origin. Of fourteen species reported from Bear Creek for the first time, only *Lexingtonia dolabelloides* is considered to be of Cumberlandian origin. Nine others, *Anodonta suborbiculata*, *Cyclonaias tuberculata* (Rafinesque, 1820), *Fusconaia ebena* (Lea, 1831), *Lampsilis abrupta*, *Lasmigona complanata complanata* (Barnes, 1823), *Potamilus ohiensis*, *Pyganodon grandis* (Say, 1829), *Quadrula quadrula* (Rafinesque, 1820) and *Utterbackia imbecillis* (Say, 1829) belong to the Ohioan fauna (Ortmann 1925, van der Schalie 1939, Stansbery 1964). Three of the previously unreported species, *Arcidens confragosus* (Say, 1829), *Strophitus undulatus* and *Toxolasma parvus*, are of unknown origin (Ortmann 1925, Stansbery 1964). The final species, *Quadrula apiculata* (Say, 1829), was apparently intentionally introduced into Tennessee River (Parmalee and Bogan 1998) and subsequently colonized Bear Creek.

Whether previously unreported species colonized Bear Creek following changes that resulted in elimination of Cumberlandian elements, or whether they were overlooked in the two earlier, abbreviated surveys, is unclear. A factor possibly resultant in finding a greater number of Ohioan species during the present study is that the earlier studies did not include downstream reaches of Bear Creek. Many Cumberlandian species typically occur in smaller streams. However, colonization of Tennessee River adjacent to Bear Creek by Ohioan species is well documented. The Muscle Shoals reach of Tennessee River was thoroughly surveyed well before its impoundment. Ten species of Ohioan or unknown origin have been recorded from the Muscle Shoals area since impoundment of the river (Stansbery 1964, Isom 1969, Parmalee *et al.* 1982, Garner and McGregor 2001). Six of the species documented from the Bear Creek system for the first time during this study were also absent from Muscle Shoals prior to impoundment. It is doubtful that these species occurred in Bear Creek, but were absent from Muscle Shoals, which had arguably the most diverse mussel fauna of modern times, with 79 species recorded (Garner and McGregor 2001).

The mussel fauna of the Bear Creek system has suffered greatly from modern perturbations to habitat. We found no evidence of 11 species historically known from there, representing 24% of the cumulative species list. However, a diverse and viable fauna remains in a short reach of the main channel. The population of *Epioblasma brevidens* in Bear Creek is the only known population of this species in the lower Tennessee River system. Only two populations of *Lexingtonia dolabelloides* remain downstream of Paint Rock River, this one and one in Duck River of middle Tennessee (Ahlstedt 1991). With concerted effort to identify and mitigate sources of impairment, we feel that the existing fauna could eventually repopulate other areas of the system. That the population includes remnants of its Cumberlandian element and one of few or the only viable population of some species in the lower Tennessee River system makes it even more valuable with respect to conservation of this group, which has suffered declines through most of its range. Furthermore, the new record of the rare, endemic *Lexingtonia dolabelloides* provides strong justification for future surveys of other small, underrepresented systems.

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Seasonal variation in the reproductive cycle of a Neotropical freshwater mussel (Hyriidae)

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Abstract: The reproductive cycle of *Castalia ambigua ambigua* in the Irituia River, Pará, Brazil, was studied between September 2000 and August 2001. Monthly random samples of mussels showed marked seasonality in the reproductive cycle with peak activity taking place at the end of the wet season. The greatest proportion of brooding females was found in May and the largest mean brood size was recorded in June. Mussels were sexually mature from 11 and 11.4 mm in females and males respectively. There was no relationship between shell length and brood size. Of the environmental data collected, only water turbidity showed a significant negative correlation with brood size. The reasons for the seasonal pattern in reproduction are discussed in the light of other studies on tropical and sub-tropical mussels.

Key words: *Castalia ambigua ambigua*, glochidia, brood size

Very little is known of the tropical freshwater mussel fauna (Bogan 1993). Due to the relatively constant temperatures of tropical areas, species may have little or no seasonal variation in their breeding cycles (Fryer 1961). While some species do reproduce throughout the year in tropical and sub-tropical areas, there is evidence from studies in Africa (Kenmuir 1981a, 1981b), Asia (Ghosh and Ghose 1972, Nagabhushanam and Lohgaonker 1978), Australia (Atkins 1979, Jones *et al.* 1986, Byrne 1998), and South America (Peredo and Parada 1986, Avelar and De Mendonça 1998, Beasley *et al.* 2000) that freshwater mussels from these areas do show seasonal variation in their reproductive cycles and that there appears to be a distinct period during which reproductive activities increase. Some species may reproduce several times a year, for example, *Caelatura mossambicensis* (Martens, 1860) and *Mutela dubia* (Gmelin, 1791) in Lake Kariba, Zimbabwe (Kenmuir 1981a), and species of *Hyridella* (Hyriidae) in southern Australia (Jones *et al.* 1986, Byrne 1998). The reasons for seasonal reproductive activity in mussels in tropical areas are not clear, but in sub-tropical areas changes in temperature appear to stimulate reproductive activity (Jones *et al.* 1986, Peredo and Parada 1986, Avelar and De Mendonça 1998, Byrne 1998). Other factors such as the trophic status of the habitat (Byrne 1998), and seasonal rains (Avelar and De Mendonça 1998) and floods (Jones *et al.* 1986) may also have a role to play.

The ability to predict seasonal variation in the reproductive cycles of freshwater mussels may be applied to their conservation and management. Knowledge of the seasonal variation in gametogenesis and glochidial brooding in *Paxyodon syrmatophorus* (Meuschen, 1781), an Amazonian species exploited for its shells (Beasley 2001), was used to recommend pauses in collecting during the reproductive period and a minimum size limit to individuals being harvested (Beasley *et al.* 2000). Other reproductive variables such as brood size may be of similar importance. Bauer (1991, 1992) has shown that the production of glochidia per female varies among European populations of freshwater pearl mussels. Such variation also appears to occur in sub-tropical freshwater mussels. Byrne (1998) found that populations of Hyriidae in Australia have marked differences in both adult shell length and brood size, depending on the trophic status of the habitat. Such differences in reproductive output were recognized by both authors to have consequences for the conservation of the populations.

Castalia ambigua ambigua (Lamarck, 1819) is a common subspecies distributed widely throughout the Amazon Basin (Bonetto 1965, Mansur and Valer 1992). The present study aimed to examine the seasonality of the reproductive cycle of *C. ambigua ambigua* using the proportion of gravid females and brood size as indicators of reproductive activity, as well as to determine the influence of environmental factors on brood size. Mussel size at the onset of sexual maturity was also determined.

MATERIALS AND METHODS

Study area

The Irituia River (47°26'5.9"W, 01°46'11.1"S at Irituia town) is located in the northeast of the State of Pará, Brazil, and extends 45 km in a northerly direction to discharge into the Guamá river near São Miguel do Guamá. The climate is tropical with a mean temperature of 25°C and relative humidity of about 85% throughout the year. The rainy period occurs between January and June and annual precipitation exceeds 2 m. The river is an important source of income for local inhabitants who commercially harvest many ornamental and food fish species as well as freshwater shrimp. Several other species of freshwater mussel occur in the Irituia River including *Triplodon corrugatus* (Lamarck, 1819), *Monocondylaea costulata* (Moricand, 1858), and *Anodontites crispata* (Bruguiére, 1792). There is no commercial harvesting of *Castalia ambigua ambigua* or other mussel species in the Irituia River.

Field sampling

Mussels were sampled monthly between September 2000 and August 2001 at three stations (A, B, and C) that were all within a radius of 2 km from Irituia town and were known by locals to contain populations of *Castalia ambigua ambigua*. Simple random sampling of populations was carried out from a small boat at each station. Marker cords and buoys divided the area into a grid 100 m along the bank by 50 m across the width of the river. Along the river bank the stretch was divided into 5 m sections whereas across the width 2 m divisions were used. A combination of letters and numbers were used to assign coordinates to the grid and 20 plots were randomly chosen each month for sampling. The same grid was sampled each month but different random plots were chosen on each occasion. The mean number of mussels per sampling plot (10 m^2) was used as an estimate of density.

At each randomly chosen plot a dive was made to obtain a sample of water from near the bottom, from which measures of dissolved oxygen (mg/l), conductivity (µS/cm), and temperature (°C) were obtained. Depth (m) was measured using a digital ultrasound depth probe and a Secchi disc with a 20 cm diameter was used to measure water turbidity (cm^{-1}). Three further dives were carried out in each sampling plot to obtain mussels using a metal box (30 x 12 x 29 cm) that was dug into the river bottom by the diver. The box was capable of retrieving approximately 2.5 l of bottom sediment at the sampling plot. Sieving of the sampled sediment was carried out using a 2 mm mesh. Animals were separated and placed over ice in a cooler and maintained at around 10°C during transport, taking care that the mussels were not in direct contact with the ice or icy water.

Laboratory analysis

Within 24 hours of collecting, a gonad biopsy was carried out to determine the sex of each individual. A syringe was used to remove fluid from the gonad. The fluid was transferred to a glass slide and examined with a light microscope for identification of the gametes. The demibranchs of females were separated from the visceral mass, taking care not to rupture the gill tissue, and stored in 70% alcohol. Each demibranch was subsequently examined using a stereomicroscope. Females were classified as brooding by the presence of a marsupium and larvae (glochidia or embryos). Undeveloped eggs were not distinguished from embryos. Demibranchs were dissected along the anterior, dorsal, and posterior edges and were gently shaken to remove all larvae, which were then transferred to a square plastic dish and counted (Beasley *et al.* 2003) directly using a stereomicroscope. The totals for the left and right demibranchs were summed to obtain the brood size for each female. All individuals sampled were measured for shell length along the anterior-posterior axis with Vernier calipers.

Statistical analysis

Data were log transformed in samples where parametric assumptions of normality and homogeneity of variances (tested using Shapiro-Wilk and F_{max} test, respectively) were violated. If variances remained significantly different after transformation, the Welch correction (Zar 1999) was applied to the procedures for the t-test and analysis of variance. Mean population density (number of mussels per 10 m^2 plot) was compared between stations, and between months, using one-way analysis of variance. Estimates of the total population size at each station were obtained by multiplying the mean density and 95% confidence interval by the total number of possible sampling units. A Chi-square test was used to compare the distribution of count frequencies with that expected from the negative binomial distribution (Fowler and Cohen 1990) and to check for differences from 1:1 in the sex ratio at each station. Two-way analysis of variance was carried out to determine if significant differences in mean brood size (mean number of embryos and glochidia per female) occurred between months of the year or between the three stations. Significant differences among individual pairs of means were located using the Tukey test. A t-test was carried out to check for differences in mean shell length between male and female mussels. Finally, Spearman rank (r_S) correlation analysis was used to investigate the relationship between brood size and female shell length, and between mean monthly brood size and mean monthly values of environmental parameters, for all three stations combined.

Table 1. Mean density, 95% confidence interval, and estimated population size of *Castalia ambigua ambigua* at the three stations A, B, and C, on the Irituia River, Pará.

	Density (no. indiv. 10 m^{-2})		Population size (No. indiv. per station)		
Station	Mean	95% c.i.	Estimated size	Min	Max
A	0.61	0.10 - 3.52	305	50	1760
B	0.53	0.08 - 3.37	265	40	1685
C	0.78	0.15 - 4.04	390	75	2020

Table 2. Numbers of males and females and chi-square statistics of the sex ratio of *Castalia ambigua ambigua* from the Irituia River at each of the three stations and for all three stations combined.

Station	Male	Female	x^2 statistics
A	76	78	0.0065, df = 1, ns
B	57	54	0.036, df = 1, ns
C	107	72	6.46, df = 1, $p < 0.05$
All three stations	240	204	2.76, df = 1, ns

Table 3. Table of analysis of variance showing the results of the two-way comparison between months and stations of mean brood size of *Castalia ambigua ambigua*.

Source of error	Df	Sum Squares	Mean Square	F	Significance
Month	10	9525826	952583	2.26	$p < 0.05$
Station	2	222680	111340	0.26	ns
Interaction Month:					
Station	10	4566188	456619	1.09	ns
Residuals	48	20188397	420592		

RESULTS

During the study period, mean density ranged between 0.5 to 1 mussels per 10 m^2 but did not vary significantly between months (F = 0.4644, df = 11, 708, ns). There were no differences in the mean density of mussels (Table 1) at any of the three stations (F = 1.534, df = 2, 475.5, ns). The variances to mean ratios at all stations were high and suggested a contagious dispersion of mussels over the river bed. The count frequency distribution was not significantly different from that expected from the Negative Binomial distribution at stations A ($x^2 = 5.6$, df = 6, ns) and B ($x^2 = 10.8$, df = 5, ns). However, at station C, there was a significant departure from this model ($x^2 = 13.8$, df = 6, $p < 0.05$). The estimated population sizes at each of the three stations were similar and ranged between 265 and 390 mussels (Table 1). The 95% confidence interval, and the minimum and maximum population size estimates based on this, indicate a skewed distribution of mussel counts (Table 1).

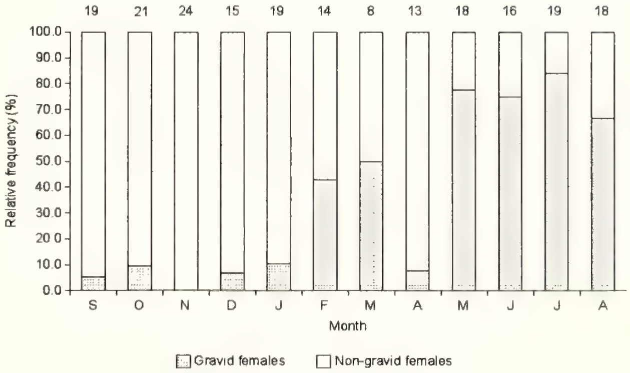

Figure 1. Relative frequency (%) of brooding and non-brooding females of *Castalia ambigua ambigua* in each monthly sample for all three stations combined. The number above each column indicates the total number of females examined.

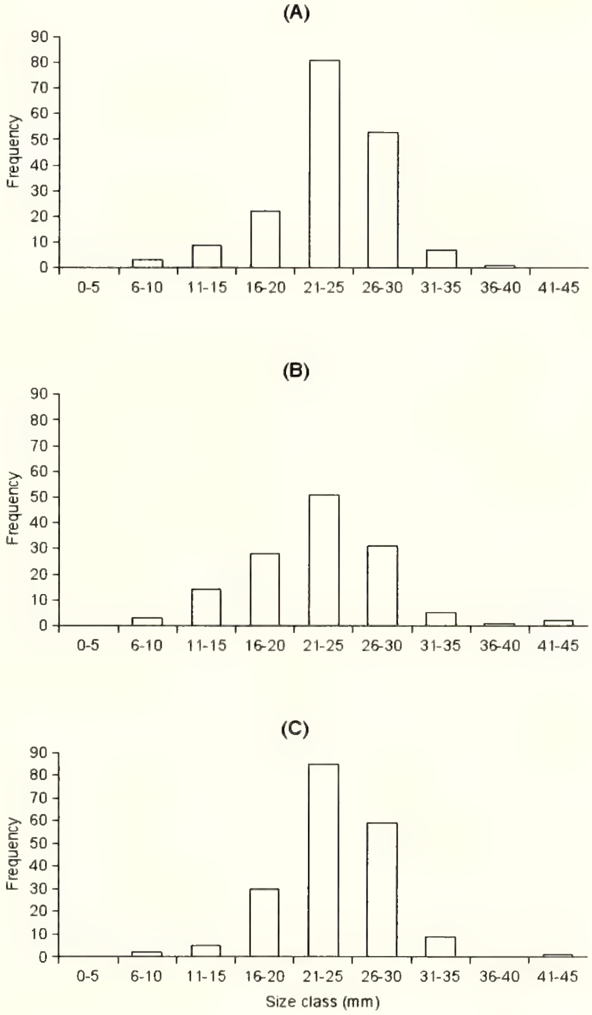

Figure 2. Population site-frequency distributions of *Castalia ambigua ambigua* from stations (A), (B), and (C) on the Irituia River.

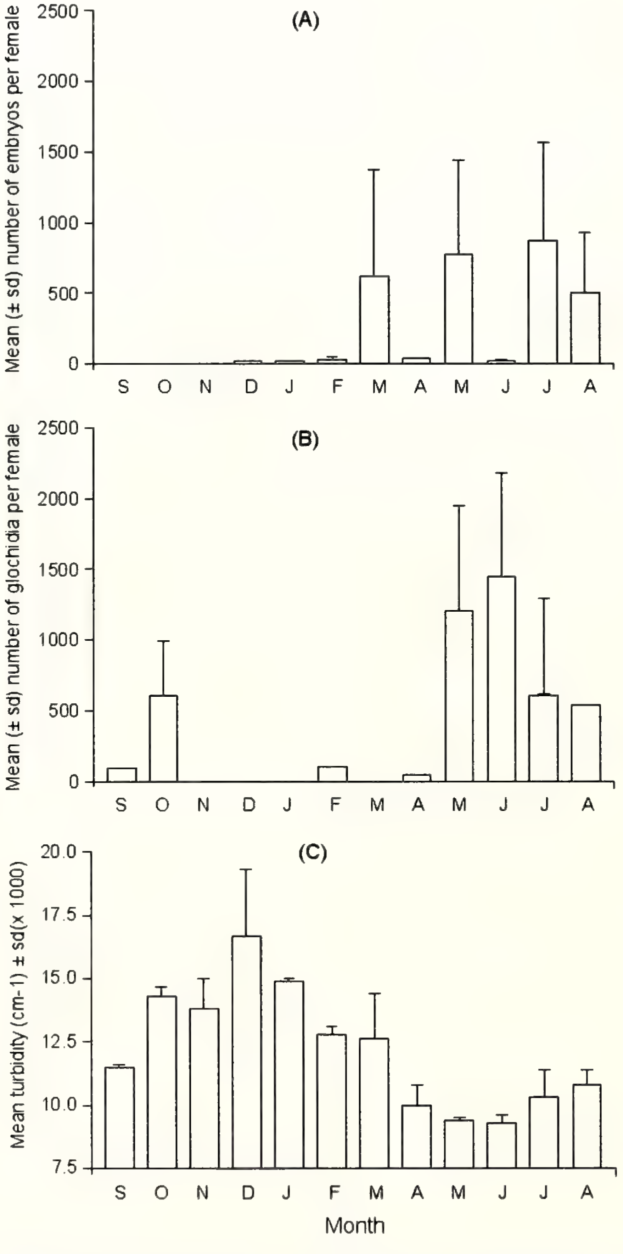

Figure 3. Mean numbers (± sd) of embryos (A), glochidia (B) of *Castalia ambigua ambigua* and mean (± sd) values of water turbidity (C) for each month for all three stations combined.

Table 4. Mean (± sd), minimum, and maximum values of environmental variables measured in the study area.

Environmental variable	Mean (± s)	Minimum	Maximum
Depth (m)	2.6 ± 0.9	0.3	6
Water turbidity (cm^{-1} x 1000)	12.2 ± 2.4	9.3	16.7
Temperature (°C)	28.4 ± 1.6	21.1	34.9
Dissolved oxygen (mg/l)	2.7 ± 0.9	0.2	6
Conductivity (µS/cm)	43.9 ± 12.9	24	110

Sex ratio and proportion of gravid females

Gravid females were found in all months except November. Between May and August, however, gravid females predominated (>60%) over non-gravid ones (Fig. 1). There were no significant differences in the ratio of males to females at stations A and B but males were significantly predominant at station C (Table 2). Individuals of indeterminate sex were found in all months except May and a single hermaphrodite was found at station A in August.

Shell length and sexual maturity

The mean (± sd) shell lengths at each of the three stations A, B and C, were 22.7 ± 4.88 mm, 21.6 ± 6.25 mm, and 23.0 ± 4.43 mm, respectively. Individuals of 5 mm or less were not found and each mussel population was mainly composed of individuals between 21 and 30 mm in length (Figure 2). The mean (± sd) shell length of sexually mature individuals of *Castalia ambigua ambigua* was 23.7 ± 4.81 mm for males and 22.7 ± 3.71 mm for females. Male mussels were significantly larger than female mussels ($t = 2.55$, $df = 445.3$, $p < 0.05$). The single hermaphrodite found measured 29 mm. There was no significant correlation between brood size and shell length of gravid females ($r_s = 0.2148$, ns). The mean (± sd) shell length of immature individuals was 14.8 ± 6.06 mm. The minimum shell length of *C. ambigua ambigua* at sexual maturity was 11.0 mm for females and 11.4 mm for males.

Brood size

The marsupium of *Castalia ambigua ambigua* is located in the posterior-ventral section of the inner demibranch. The minimum, mean, and maximum brood sizes of *C. ambigua ambigua* encountered during the study period were 14, 725, and 3023 larvae per female, respectively. Mean brood size was low between September and April, higher between May and August, and the maximum value occurred in June. A significant difference in mean brood size was found between the months of February (51 larvae per female) and June (1020 larvae per female) (Tukey HSD, $p < 0.05$) (Table 3). Mean numbers of embryos per female were high in March, May, July, and August (Figure 3A), whereas the mean number of glochidia per female was high in October and between May and August (Figure 3B). Embryos predominated over glochidia in March and July whereas glochidia predominated in October, May, and June. No differences in mean brood size were found between stations (Table 3). At stations A, B, and C, the mean brood sizes were 587, 681, and 840 larvae per female, respectively. The interaction between month and station was not significant (Table 3), indicating a similar seasonal pattern of variation in mean brood size at each station.

Environmental data

Environmental data for the study area are summarized in Table 4. Mean water turbidity was negatively correlated with mean brood size during the study period ($r_s = -0.73$; $p < 0.01$), with largest brood sizes occurring during the drier months with low turbidity. None of the other environmental parameters were significantly correlated with mean brood size. Depth increased during the rainy season whereas water turbidity increased due to the increase in the level of suspended solids in the river. Mean water temperature was relatively constant (27-29°C) during the entire year but was higher during October and November, the final months of the dry season. Dissolved oxygen was constant between September and March but dropped considerably in February, only to rise again during the subsequent six months. Conductivity values were highest at the end of the dry season, in December, and declined until the middle of the wet season, in March, after which values began to rise again.

DISCUSSION

In general, the sex ratio of *Castalia ambigua ambigua* did not differ from 1:1 and only a single hermaphrodite was recorded. This was also the case for a population of *Cyclonaias tuberculata* (Rafinesque, 1820) in the Tennessee River, USA (Haggerty *et al.* 1995). Dillon's (2000) review of sex ratios in unionoid mussels showed most populations did not differ from 1:1. In contrast, Byrne (1998) found that populations of *Hyridella depressa* (Linnaeus, 1758) in southeastern Australia were skewed in favor of female microhermaphrodites (predominantly female gonads with small amounts of spermatogenic tissue) and suggested that this may be a response to low population density, such as that described by Bauer (1997) for the freshwater pearl mussel. Female microhermaphrodites are found in populations of *Utterbackia imbecilis* (Say, 1829) in which high rates of self-fertilization occur (Johnston *et al.* 1998). Nagabhushanam and Lohgaonker (1978) found that *Lamellidens corrianus* (Prasad, 1922) is a simultaneous hermaphrodite, but shows little synchrony between mature male and female follicles of individual mussels, thus the chances of self-fertilization are low. On the other hand, *Lamellidens marginalis* (Simpson, 1900), another Indian freshwater mussel, was found to be dioecious (Ghosh and Ghose 1972).

Among South American Hyriidae there is much variation with respect to sex ratio and hermaphroditism. A population of *Paxyodon syrmatophorus* in Brazil was found to be predominantly male with a very low incidence of hermaphrodites (Beasley *et al.* 2000). *Diplodon rotundus gratus* (Wagner, 1827) was shown to be a functional hermaphrodite all year round (Avelar and De Mendonça 1998), although hermaphrodites predominate at the end of summer and during autumn whereas females predominate in spring and summer. In *Castalia undosa undosa* (Martens, 1827), hermaphrodites are rare (Avelar and Santos 1991) whereas in *Diplodon chilensis chilensis* (Gray, 1828), no hermaphrodites were found (Peredo and Parada 1984). Dillon (2000) suggests that sexuality in unionoid mussels may have a large environmental component, and skewed sex ratios and hermaphroditism are more likely to occur when there is fertilization failure. The equal sex ratios and lack of hermaphrodites in Irituia populations may be due to the fact that the mussels are spatially aggregated and there are high rates of fertilization in females. At station C, the sex ratio was skewed in favor of males and, being located 1 to 3 km upstream of stations B and A, respectively; station C may experience lower fertilization rates because of the loss of spermatozoa due to downstream water flow.

Castalia ambigua ambigua appears to be reproductively active during the entire year because glochidia and embryos were found during practically the entire study period. Similarly, gametes were found in all monthly biopsies, suggesting year-round gametogenesis in *C. ambigua ambigua*. The latter phenomenon appears to be common in North American *Anodonta* spp. (Heard 1970) and in freshwater mussels in both tropical (Ghosh and Ghose 1972, Nagabhushanam and Lohgaonker 1978, Beasley *et al.* 2000) and sub-tropical habitats (Jones *et al.* 1986, Peredo and Parada 1986, Avelar and De Mendonça 1998, Byrne 1998). We did not attempt to evaluate seasonal variation in gametogenesis, however, studies of other tropical freshwater mussels indicate that, although gametogenesis occurs throughout the year, there is a distinct increase in gamete production at certain times of the year (Ghosh and Ghose 1972, Nagabhushanam and Lohgaonker 1978, Beasley *et al.* 2000). Although gametogenesis begins at the end of spring and continues through the summer, the peak reproductive period of *Diplodon rotundus gratus* in sub-tropical Brazil is confined to the autumn when mature oocytes and sperm occur simultaneously; only during this period were fish found that were infected with glochidia (Avelar and Mendonça 1998). The Australian hyriid *Cucumerunio novaehollandiae* (Gray, 1834) also undergoes year-round gametogenesis but peak reproductive activity is associated with the warmest months of the year (Jones *et al.* 1986). The gonads of *Lamellidens marginalis* in tropical India are active during most of the year, particularly so during the rainy season, after which there is a short inactive period of 2 months (Ghosh and Ghose 1972). Peak gametogenic activity and spawning occurred in *Lamellidens corrianus* between September and December, months in which temperature decreases (Nagabhushanam and Lohgaonker 1978).

There was marked seasonality in the proportion of gravid females and mean brood size of *Castalia ambigua ambigua* in the Irituia River, with peak numbers of gravid females and larvae occurring between May and June, the end of the wet season. Beasley *et al.* (2000) found that peak numbers of gravid females of *Paxyodon syrmatophorus* in the Tocantins River also occurred at the end of the wet season, suggesting that seasonal variation in reproductive cycles does occur in tropical freshwater mussels. The population density of *C. ambigua ambigua* did not vary significantly in the Irituia River throughout the year and thus seasonal differences in reproductive activity must be due to environmental factors.

We found that water turbidity was negatively correlated with brood size. It is unlikely that mussels use light *per se* as an environmental cue but they may use other environmental cues linked to a decrease in turbidity, such as a decrease in suspended solids, rainfall, or current speed, as signals to begin or intensify reproductive activities. This strategy may have adaptive value as the water level falls and thus lower water volume may allow a greater number of successful fertilization events. Kenmuir (1981a) noted regional differences in the timing of reproduction in *Aspatharia walbergi* (Krauss, 1848), a species that reproduces once a year, in two lakes in Zimbabwe at different altitudes and with different temperature regimes. Kenmuir (1981a) further suggested that seasonal water currents may act as a stimulus for reproduction in this species. Avelar and De Mendonça (1998) found that heavy rains coincide with peak reproductive activity in *Diplodon rotundus gratus* and a similar situation was described for *Cucumerunio novaehollandiae* (Jones *et al.* 1986) and *Hyridella depressa* (Byrne 1998), with gametogenesis being stimulated by higher current speeds or perhaps abruptly cooler water temperatures. In Brazil, seasonal migrations of fish (*piracema*) coincide with the rainy season and flood waters and are linked to the reproductive cycle of freshwater mussels such as, for example, glochidial release in *Diplodon martensi* (Ihering, 1893) (Mansur 1999). On the other hand, Atkins (1979) reported highest numbers of glochidia of *Hyridella drapeta* (Iredale, 1934) encysted on fish during the warmest months of the year in Victoria, Australia. Reproductive activities may also be influenced by the trophic status of the habitat. Populations of *H. depressa* at eutrophic sites in southeastern Australia were characterised by continuous gametogenesis whereas mussels at oligotrophic sites tended to show seasonal gametogenesis (Byrne 1998). At one of the latter populations, reproductive failure was common and the author suggested that phytoplankton availability may directly influence the seasonality of reproductive activity. In North American freshwater mussels, gametogenesis may extend into the autumn and winter months through modified temperature regimes influenced by upstream dam waters (Jirka and Neves 1992).

In the Irituia River, male mussels were significantly larger than female mussels. Heard (1970) found this type of cryptic sexual dimorphism, which can only be determined by measurements and statistical comparison, in some species of *Anodonta*. A more obvious example of sexual dimorphism in *Castalia undosa* has been recorded by Avelar *et al.* (1991). No dimorphism was found in the hyriid *Diplodon chilensis* (Peredo and Parada 1984). There was no significant correlation between brood size and shell length of gravid females in *Castalia ambigua ambigua*. This is probably because marsupia were in different stages of development (filling, full, emptying) within the population on each sampling occasion. Reproductively active *C. ambigua ambigua* in the Irituia River were small in comparison with other species of Hyriidae (Peredo and Parada 1986, Byrne 1998, Beasley *et al.* 2000), although direct comparison is not always possible due to size-selective sampling in other studies. Small size at maturity (early sexual maturity) may be selected for by low mortality in the early stages of life (Dillon 2000) because investment in reproductive activity is greater than investment in growth. Parada *et al.* (1989) found that growth was slower in summer in *Diplodon chilensis*, during which period peak gametogenesis and glochidial brooding occur (Peredo and Parada 1986). Thus, in some cases, investment of energy in growth may alternate with investment in reproduction. This may be a common strategy in tropical and sub-tropical areas where temperature does not vary sufficiently to inhibit growth, as occurs in winter in temperate areas.

Consequences for conservation

Individuals of *Castalia ambigua ambigua* in the Irituia River had small brood sizes in comparison with members of other families of unionoideans and other Hyriidae (Parada *et al.* 1990, Jupiter and Byrne 1997, Byrne 1998, Beasley pers. obs.). Furthermore, *C. ambigua ambigua* from the Irituia River were smaller (mean shell length: 21.6 - 23.0 mm) than conspecifics from the Tocantins River, where the mean shell length at five sites varied between 34 and 45 mm and the mean length of mussels harvested for button manufacture was around 60 mm (Beasley 2001). Preliminary assessment of the brood size of *C. ambigua ambigua* from the Tocantins River suggests that mean brood size is greater in these larger individuals (Beasley pers. obs.). The mean brood size of three individuals from the Tocantins River that measured between 27.2 and 38.4 mm was 1813 larvae.

Bauer (1991, 1992) has shown that, in European populations of the freshwater pearl mussel, small females produce small brood sizes. This also appears to be true for tropical and sub-tropical mussels. For example, Byrne (1998) shows a clear site-specific relationship between shell length and mean brood size in *Hyridella depressa*. Because reproductive output is low in populations with small individuals, the adverse effects of environmental degradation and/or harvesting may be greater. If this is shown to be the case, practical conservation and management strategies should be directed towards such priority populations (Bauer 1991). However, multicyclic (repetitive breeding) reproductive strategies (Dillon 2000) and earlier sexual maturity may compensate for low reproductive output in populations with small individuals. Although no municipal water quality data are available, the Irituia River appears not to receive large inputs of pollution, due to the lack of industry and sparse urban development in the catchment. Young mussels were regularly found in small numbers throughout the year in the Irituia River, indicating that post-larval settlement is successful to some extent. The population sizes of *Castalia ambigua ambigua* did not differ between stations and thus the impact of pollution from Irituia town does not appear to have an adverse effect on the population at station B. Thus, the prospects for the survival of populations of *C. ambigua ambigua* in the Irituia River are good.

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Growth of *Megalobulimus mogianensis* (Gastropoda: Megalobulimidae) raised in the laboratory from hatching to adulthood

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Abstract: This study establishes absolute and relative growth curves for the snail *Megalobulimus mogianensis* raised in the laboratory from hatching to adult. A preliminary study indicated that shell length is a precise and practical linear measurement for predicting other body dimensions. In an indoor terrarium where photoperiod, temperature, and humidity varied in parallel to natural fluctuations, individuals of *M. mogianensis* whose shell length at hatching ranged from 19.4 to 29.3 mm, required one to three years to become adults with shell lengths ranging from 78.8 to 99 mm. These animals showed a pronounced seasonal pattern of high growth rate during the warm summer months, with a decline in autumn and no growth in winter. A statistically significant positive correlation between relative growth rate and temperature was detected (Spearman, $p < 0.002$). The growth rate of poikilotherms tends to increase with temperature as a result of an increase in metabolic rate. The maximum relative growth rate, highest in the youngest snails, decreased with increasing age and size. This can be explained by a decrease in metabolism that is related to a decrease in surface to volume ratio occurring as the animal grows. As the animals became adults, an increased allocation of energy from somatic growth to reproductive activity may also have occurred. How factors other than temperature and body size influence the growth of *M. mogianensis* remains to be investigated.

Key words: Mollusca, allometry, absolute and relative growth.

Megalobulimus mogianensis Simone and Leme, 1998 (= *M. sanctipauli sensu* Romero and Hoffmann 1991 non Ihering and Pilsbry 1900) is a tropical land snail that has a seasonal activity pattern starting in the warm rainy season (spring-summer) and decreasing toward the dry cold season (autumn-winter), when the snails dig into the ground for a period of dormancy from which they awaken the following spring. This species is currently being investigated in our laboratory using behavioral and physiological approaches (Romero and Hoffmann 1988, 1991a, 1991b, 1992, 1996, Romero *et al.* 1994, Rizzatti and Romero 2001). Information on aging is very important and may add to our overall understanding of the biology of this snail.

Growth rate can often be estimated directly from field data by the size-frequency distribution method. However, this method requires a great abundance of animals and individuals of *Megalobulimus mogianensis* are very sparsely distributed in nature. Since laboratory rearing is difficult, tedious, and labor intensive, and because survival is scarce, no experimental data are available in the literature about the development of these snails and the time from hatching to adult size (Romero 1998). There are no reports of the allometric relationships for these snails.

The present paper reports results from a study on the absolute and relative growth of the snail *Megalobulimus mogianensis* raised in the laboratory from hatching to the adult stage.

METHODS

Animals

Romero (1998), Romero and Hoffmann (1991a, 1991b, 1992, 1996) and Romero *et al.* (1994) identified specimens of *Megalobulimus* from Santa Rita do Passa Quatro (21°40'S, 47°30'W), State of São Paulo, Brazil, as *Megalobulimus sanctipauli* according to Silva (1985). However, a recent study by Simone and Leme (1998) has revealed that these animals belong to the species *Megalobulimus mogianensis.*

Twenty to thirty adult specimens of the land snail *Megalobulimus mogianensis* were collected each year in Santa Rita, kept at ambient temperature in outdoor terraria flushed with tap water, and fed green leaves and wheat bran *ad libitum* once a day. Oyster powder was provided as a source of calcium and magnesium. Adults laid eggs in the warm and rainy months (November to April) of the year. At hatching the snails were individually marked, measured, weighed, and kept in plastic boxes (29 x 29 x 14 cm) filled with a 6-8 cm layer of a moist mixture of soil and sand (3:1). Each box (containing ≤ 25 newly-hatched snails or 4-7 snails with $35 <$ length < 60 mm or 2-3 snails with $60 <$ length < 90 mm or 1 snail > 90 mm) was covered with plastic mesh. Excreta and food remains were removed daily except on weekends, the soil was stirred and sprayed with water, and fresh food was supplied *ad libitum.* Since ingesting a mixed diet is thought to provide a more balanced nutrient regimen (Foster *et al.* 1999), the snails were fed green leaves (lettuce and wild chicory) dusted with oyster powder and wheat bran was supplied once a week. The boxes were kept in an indoor terrarium where photoperiod, temperature, and humidity varied in parallel to natural fluctuations during the course of the study, from November 1994 to April 1999. Temperature and humidity were recorded with maximum/minimum thermometers and a dry-wet hygrometer, respectively, throughout the experimental period and their mean values are shown in Fig. 1.

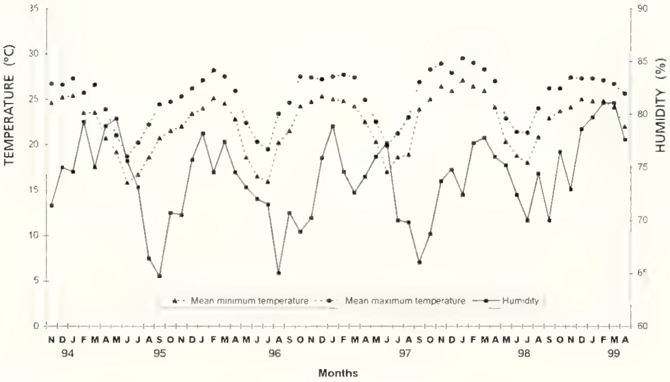

Figure 1. Mean maximum and minimum temperatures and relative humidity in the indoor terrarium throughout the experimental period.

Allometric relationships

To determine whether shell length is a suitable and convenient measurement to assess growth rate in *Megalobulimus mogianensis*, individual measurements of shell length (SL), shell width (SW), and whole body weight (BW) were made on animals newly hatched in the laboratory ($n = 133$), snails of different sizes/ages growing in the laboratory or collected in nature ($n = 38$), and adult specimens collected in nature ($n = 118$). The whole live body weight of the snail was determined to the nearest 0.1 g by means of a Record Balance (model 1001). The length (the maximum distance along the long axis of the shell) and width (the maximum distance along the short axis of the shell), were determined with a Vernier caliper (0.01 mm precision). These data were used to determine the fit of the parameters to the allometric growth equation:

$$y = a\,x^{b} \text{ (or } \log y = \log a + b \log x\text{)}$$

where x is some measure of a part of the body, y is a measure of the whole body or another part, and *a* and *b* are constants estimated from a set of data using the least squares method (see White and Gould 1965).

Absolute and relative growth

To determine the absolute and relative growth, measurements were made on animals hatched from November 1994 to March 1996 and were extended until April 1999, 45 days after the last animal became an adult. The development of a reflected lip on the peristome of the shell was considered to denote adulthood (Pollard *et al.* 1977, Stiven and Foster 1996, Iglesias *et al.* 1996, Mora 1998). The measurements were made at hatching and approximately every 15 days until adulthood, except where otherwise indicated. For the animals hatched in 1994 and 1995 the measurements were interrupted during mid-autumn/winter (from April 18 to October 3). During this period of low temperatures the snails were allowed to enter into dormancy while the soil of the plastic box was allowed to dry concomitantly with the fall of environmental humidity. A subset of the animals hatched in 1996 were allowed to enter into dormancy and a subset were kept active during mid-autumn/winter. The latter animals were stimulated by spraying with water and feeding daily. The measurements during autumn/winter were made approximately every 30 days, except where otherwise indicated.

According to Murray (*in* Wilbur and Owen 1964), from a physiological viewpoint, relative growth rather than absolute growth is the more useful mode of representation in that the growth increments are expressed in terms of the unit of tissue that produced them. Thus, relative growth rate for each snail that became an adult was calculated on each measurement date, from hatching to adult age, according to the equation $L_2\text{-}L_1/L_1(t_2\text{-}t_1)$ where L_1 is the initial length, L_2 is the final length and $t_2\text{-}t_1$ is the time in days between consecutive measurement dates (Wilbur and Owen 1964). Associations between relative growth rate and mean minimum and mean maximum temperature during the increment period were explored by the nonparametric Spearman rank correlation coefficient, with the level of significance set at $p \leq 0.05$.

RESULTS

Allometric relationships

The shell length at hatching ranged from 19.4 to 29.3 mm ($\bar{x} = 24.1 \pm 0.2$, $n = 133$). In the snails of intermediate age, shell lengths ranged from 23.6 to 93.6 mm ($n = 38$). The shell lengths of adults collected in nature ranged from 81 to 100.5 mm ($\bar{x} = 90.4 \pm 0.3$, $n = 118$). Table 1 gives the allometric equations for three body dimensions of *Megalobulimus mogianensis*. In addition, this table provides the number of pairs of data used (n) and the correlation coefficient (r), which gives an estimate of how well the data fit the allometric model. The relationships between width and length have

Table 1. Allometric equations for three dimensions of *Megalobulimus mogianensis*. SL= shell length, SW = shell width, BW = body weight, r = correlation coefficient, n = number of individuals.

Relation	n	Equation $Y = ax^b$	Transformation $\log y = \log a + b \log x$	r (%)
SW x SL	289	$SW = 1.2968\ SL^{0.8181}$	$\log SW = 0.1129 + 0.8181 \log SL$	99.8
BW x SL	285	$BW = 0.0009\ SL^{2.620}$	$\log BW = -3.0458 + 2.620 \log SL$	99.7
BW x SW	285	$BW = 0.0004\ SW^{3.1948}$	$\log BW = -3.3979 + 3.1948 \log SW$	99.7

been found to be of a linear type ($b = 0.82$), whereas weight-length ($b = 2.62$) and weight-width ($b = 3.19$) relationships followed a cube law. High r values are noted for relationships based on length as the independent variable, which also has the advantage of a much greater range of values than width. So, as shown for other molluscs (see Hickman 1979), shell length of *M. mogianensis* provides a useful, precise, and practical linear measurement for predicting the other body dimensions and thus to assess growth rate in this species.

Absolute and relative growth

Figure 1 describes the climatic conditions from November 1994 to April 1999 in the indoor terrarium. The mean values of relative humidity and minimum and maximum temperatures were very similar each year. The lowest temperatures occurred in June-July (minimum: 15.8 to 18.0°C; maximum: 18.7 to 21.3°C) and the highest temperatures occurred in January-February (minimum: 25.1 to 27.1°C; maximum: 27.3 to 29.5°C), except in 1998 when the highest temperatures occurred in November. The lowest mean humidities (64.7 to 70%) occurred in August-September and the highest humidities occurred in January-March (78.2 to 81.1%).

Of the initial 21 snails hatched in 1994 only one became an adult (4.8%). In the 1995 cohort, of 35 animals hatched just one became an adult (2.9%). In 1996, 152 animals hatched but only 4 became adults (2.6%).

A large number of animals died before the first dormancy period (48%, 1994 cohort; 77%, 1995 cohort; and 50%, 1996 cohort). Just after the first winter most of the snails were dead (71.4%, 1994 cohort; 94.3%, 1995 cohort; 92.1%, 1996 cohort). In the 1996 cohort all the snails that became adults were fed during autumn-winter. Studies on the population dynamics of the land snail *Helix texta* Mousson,1861 have revealed that survival of the young is very low and most of them (90%) do not survive the first year due to the winter cold and to the summer drought, perhaps because juveniles are not yet equipped with cold-resisting physiological mechanisms (Heller and Ittiel 1990).

Figure 2 shows the absolute growth expressed as shell length as a function of age expressed as months for the two overwinter-starved snails that became adults in the indoor terrarium. The curves for both animals are sigmoidal, with initial growth being followed by a period of no growth when the animals entered into dormancy. Growth resumed about six months later and ceased when the adult shell morphology was attained. This size was 98.95 mm at the age of 15.7 months (1.7 year) for the snail hatched in 1994 and 93.1 mm at the age of 13.4 months (1.1 year) for the snail hatched in 1995. Figure 3 shows similar absolute growth curves for the 4 snails from the 1996 cohort that became adults. These overwinter-fed animals also underwent periods of no growth similar to those observed in the animals that were starved over the winter. Adult sizes of 78.75, 88.95, 89.15, and 90.65 mm were attained at 28.8, 26.0, 36.5 and 14.0 months, respectively (1.2 to 3 years). For each animal the seasonal changes in growth resulted in an annual sigmoidal curve.

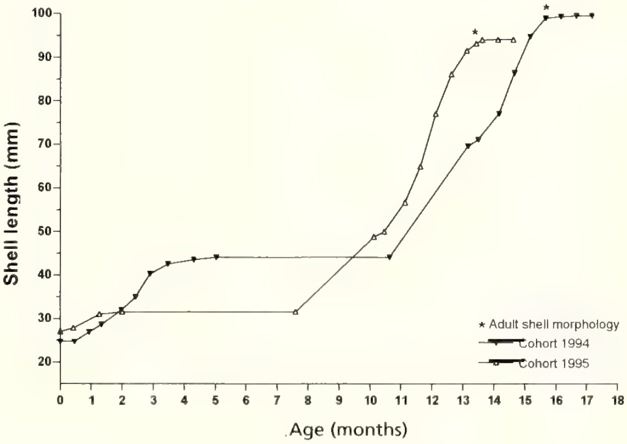

Figure 2. Absolute growth expressed as shell length as a function of age expressed as months for the two overwinter-starved snails that became adults.

Feeding during the period of low temperature (autumn-winter) did not accelerate the time or increase the size required to attain adulthood. Thus, in the indoor terrarium, where photoperiod, temperature, and humidity varied in parallel to natural fluctuations, *Megalobulimus mogianensis* took from 1 to 3 years to reach adulthood, with shell length ranging from 78.8 to 99 mm. This size range is very close to that obtained for adults collected in the field (81-100.5 mm).

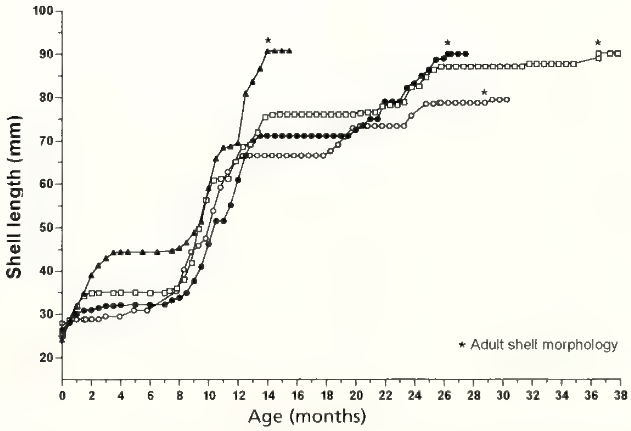

Figure 3. Absolute growth expressed as shell length as a function of age expressed as months for the four overwinter-fed snails (1996 cohort) that became adults.

Figure 4 shows the relative growth rates as well as the mean minimum and maximum temperatures for each animal that became an adult. Growth was not uniform throughout the year. In the animal from the 1994 cohort, for example, the relative growth rate increased from December to February when a maximum value was attained. A marked decrease in growth rate followed, which reached its lowest value in April when the snail was allowed to enter into dormancy. The animal was measured again at the end of winter (early October), when its length was the same as that recorded at the beginning of dormancy (see Fig. 2). A second slightly lower peak of growth occurred in December and February 1996, after which the growth decreased again to its lowest value in April, just after the animal had become an adult. Similar curves are shown for the other animals from the 1995 and 1996 cohorts. Relative growth rate tended to decrease with

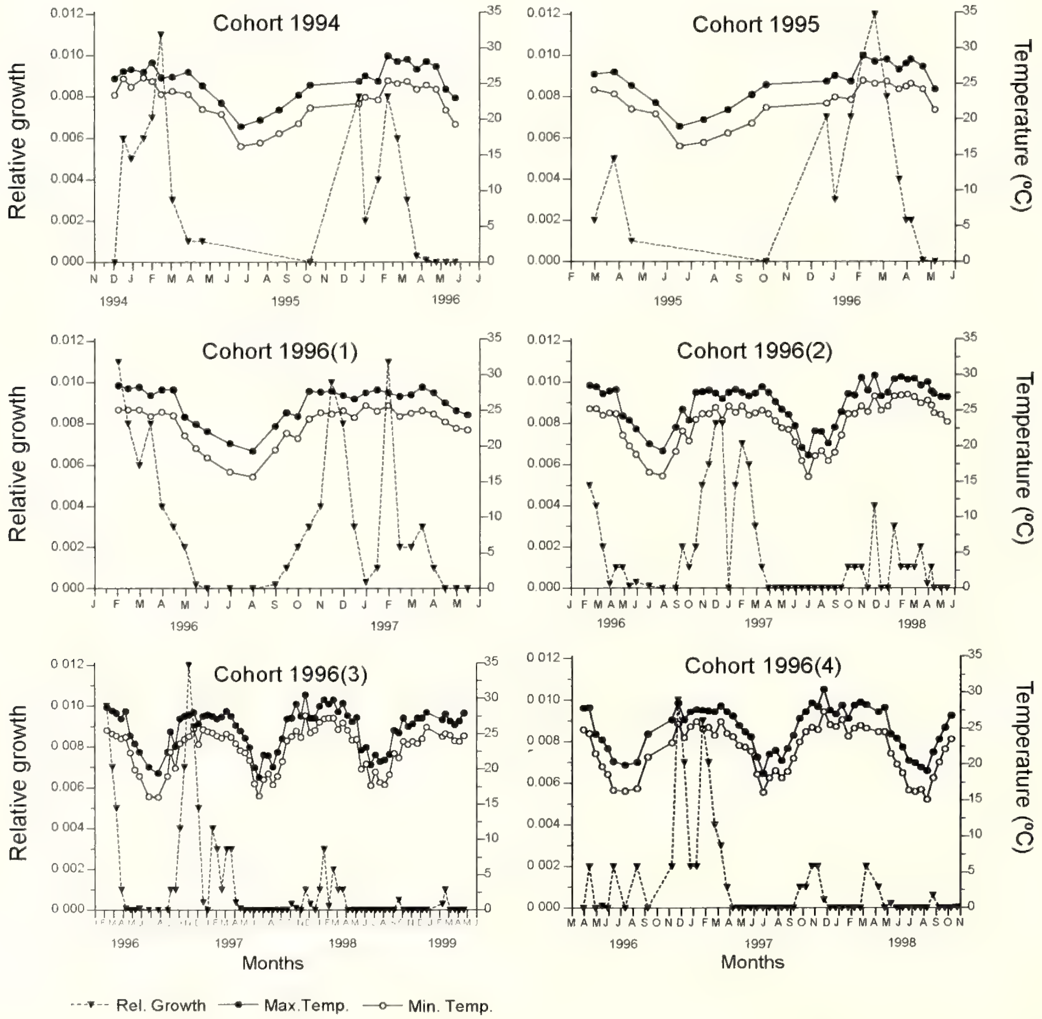

Figure 4. Individual relative growth rates from hatching to adult together with mean minimum and maximum temperatures for the years in which each animal became an adult. Relative growth rate = $L_2-L_1/L_1(t_2-t_1)$ where L_1 is the initial length, L_2 is the final length, and t_2-t_1 is the time in days between consecutive measurement dates.

increasing age or size, with the lower values occurring toward the period when the animals became adults.

Growth was very closely related to temperature in all of the experimental animals. Increasing temperature during the period from September and October to January and February (spring-summer) accelerated growth, while a marked decrease in growth rate coincided with the period of the decrease in mean minimum and maximum temperatures from March to June (autumn). With the exception of snail 4 from the 1996 cohort, whose relative growth rate oscillated close to zero during its first winter, all of the experimental animals including the fed ones stopped their growth during winter conditions (July-September). A statistically significant positive correlation between relative growth rate and temperature was detected for all the experimental animals (Spearman, $p < 0.002$).

DISCUSSION

This study establishes absolute and relative growth curves for the snail *Megalobulimus mogianensis* raised in the laboratory from hatching to adulthood. A preliminary study on allometric relationships indicated that length is a suitable and convenient linear measurement for predicting other body dimensions and thus to assess growth rate in this species. The relationship between width and length in this species is linear ($b = 0.8$) whereas weight-length ($b = 2.6$) and weight-width ($b = 3.2$) relationships follow a cube law. Tokeshi *et al.* (2000) detected values of b ranging from 2.7 to 3.5 for regressions of total weight on shell size for 29 molluscan species. These results support the general observation of Wilbur and Owen (1964) that when length is the reference parameter x, and y is weight, the values for b lie between 2.5 and 4.5. This occurrence is a simple consequence of elementary geometry: volume increases as the cube of linear dimensions (Gould 1966).

In the indoor terrarium, where photoperiod, temperature, and humidity varied in parallel to natural fluctuations, *Megalobulimus mogianensis*, whose shell length at hatching ranged from 19.4 to 29.3 mm, required one to three years (13 to 36 months) to reach adulthood, with shell length ranging from 78.8 to 99 mm. This size range is very close to that obtained for adults collected in the field. The time needed to reach adult size agreed with data from several authors cited by Pollard *et al.* (1977), who found that the average duration of the juvenile period of laboratory-reared *Helix pomatia* Linnaeus, 1758 ranges from 2 to 4 years. *Mesodon normalis* (Pilsbry, 1900) requires approximately 2 years to reach adult size (Foster and Stiven 1996). Similarly, the snail *Bradybaena fruticum* (Müller, 1774) reaches sexual maturity, externally indicated by the formation of a lip at the aperture, 21 months after hatching (Staikou *et al.* 1990). According to Lazaridou-Dimitriadou and Saunders (1986), *Helix lucorum* Linnaeus, 1758 is sexually mature by three and rarely by two years after hatching.

The large variations in time to adulthood and size are expected. Growth can vary greatly within a population and even among individuals from the same brood (Wilbur and Owen 1964). Genetic or environmental differences or their interactions may explain growth rate differences (Desbuquois 1997).

All the animals that became adults showed the same pronounced seasonal pattern of high growth rate during the warm summer months, declining through autumn and stopping in the winter. Despite unlimited access to food, overwinter-fed animals also ceased to grow during this period of low temperatures. A slow or null shell growth during winter has been reported for many freshwater snails (see Costil and Dagusan 1995). A positive correlation between relative growth rate and temperature was detected for all the experimental animals. This is in agreement with the findings of various authors for several molluscan species (Broom and Mason 1978, Hickman 1979, Holopainen 1980, Aviles and Shepherd 1996, Nie *et al.* 1996, Jess and Marks 1998).

Generally speaking, the growth rate of poikilotherms tends to increase with temperature as a result of the increase in metabolic rate, provided enough food is available (Broom and Mason 1978). Below a given temperature, feeding ceases, the digestive tract becomes empty, and growth is very slow or absent (Wilbur and Owen 1964). Thus, if temperature is too low, presumably even excess food will not result in increased growth (Broom and Mason 1978). This may be the reason for the cessation of growth during autumn and winter in the snails kept active and fed. The decrease in growth rate with age or size is a general characteristic of organisms (Wilbur and Owen 1964) and has been described for several species of molluscs (Brousseau 1979, Hickman 1979, Shpigel *et al.* 1996, Plaut *et al.* 1996). It can be explained by a decrease in metabolism that is related to a decrease in surface to volume ratio occurring as the animal grows (see Gould 1966). Toward the period when the animal becomes an adult an increased allocation of energy from somatic growth to reproductive activity may also occur (Holopainen 1980, Shepherd and Hearn *in* Capinpin and Corre 1996, Keas and Esch 1997).

In addition to temperature and body size, there are a multitude of factors, both genetic and environmental, that can affect growth (Holopainen 1980). How these factors influence the growth of *Megalobulimus mogianensis* remains to be investigated.

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Synchronized sculpture in gastropod shells

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Abstract: Synchronized sculptures on gastropod shells are periodic sculptures built at fixed angular intervals around a single whorl, and/or at consistent reciprocal positions on successive whorls. They occur in several gastropod families, and have a varied adaptive significance, which includes stabilizing the organism during locomotion, facilitating righting after accidental overturning, enhancing the clamping action against a substrate, and increasing the overall strength of the shell. Regulatory processes are apparently involved in the construction of synchronized sculpture, and in particular in ensuring the proper alignment of sculptural elements across successive whorls. In most instances, observations support the idea that the main factor controlling this synchronization is a tactile feedback provided by the mantle tissues touching the sculpture on the external surfaces of earlier whorls.

Key words: functional morphology, morphogenesis, pattern formation, evolution, Mollusca

Gastropod shells are in direct contact with the soft parts of the organism, and usually also with the surrounding environment. As a consequence, gastropod shell geometry and surface relief are important in several adaptive contexts, especially related to locomotion, feeding, and defense from predators (Kohn *et al.* 1979, Signor 1982a, 1982b, Savazzi 1989, 1991, 1994, Paul 1991, 1999, Kohn 1999, below).

Most gastropod shells are helically coiled and consist of several whorls. In the large majority of species, each whorl is cemented onto and partly overlaps the preceding whorl. In many gastropods, the shell bears a strong external relief composed of individual sculptural elements that are arranged in a periodic fashion. In several cases, albeit not always, these sculptural elements appear to be located at consistent reciprocal angular intervals around a single whorl, and/or at consistent reciprocal positions on successive whorls. This geometric regularity is evident to observers, and as a result it has been noted by numerous authors, including early ones. In several cases, this is reflected in generic or subgeneric names, like *Biplex* Perry, 1811 (= two folds [per whorl]), *Triplex* Perry, 1810 (= three folds), and *Hexaplex* Perry, 1811 (= six folds), as well as specific epithets like *tripterus*, *trialatus*, *quadricostata*, *tetragona*, *quinqueplicata*, *hexagonus*, and *heptagona*.

In other cases, although sculptural elements are arranged at relatively regular angular intervals to other elements located on the same whorl, they do not match the arrangement of corresponding elements on earlier or subsequent whorls (see also below). This paper concentrates on the former type of sculptural pattern, and presents an analysis (albeit not an exhaustive survey) of their occurrence among gastropods, of the adaptive significance of these features, and of the biological mechanisms that are likely involved in the construction of these patterns.

MATERIALS AND METHODS

Recent and fossil gastropod shells were studied by the authors in several museum and university collections. The main repositories of illustrated specimens are abbreviated as follows in the figure captions: ES, specimens in the possession of Enrico Savazzi at Institute of Earth Sciences, Uppsala University, Uppsala, Sweden; NHM, Department of Palaeontology, The Natural History Museum, London, UK; NSMT, National Science Museum, Tokyo, Japan; SMNH, Department of Invertebrate Zoology, Swedish Museum of Natural History, Stockholm, Sweden; CU, Department of Earth Sciences, Cambridge University, Cambridge, UK; UMUT, University Museum, University of Tokyo, Tokyo, Japan.

The names of additional repositories are indicated in full in the figure captions. Specimen/lot numbers are indicated when available. Shells were gold sputtered prior to SEM observations. Unless otherwise indicated in the figure captions, sizes refer to shell heights.

GENERAL PROBLEMS AND CONCEPTS

Defining, recognizing, describing, and explaining synchronized sculpture in gastropods involves a few general problems, which are addressed in this section. Sculptural patterns in which elements are located at precise reciprocal positions over a large portion of the shell are particularly interesting from a morphogenetic, constructional, and functional point of view. In most cases, this ordering results in sculptural features on successive whorls being aligned (or placed at specific angular intervals) with respect to each other. This phenomenon can be called *juxtaposition*. As used in this paper, this term is descriptive, and indicates only a recognizable, regular geometric ordering. It carries no implication about the existence or nature of any regulatory mechanism involved in the construction of the sculpture.

In the context of shell growth, the construction of this type of pattern may be expected to involve a morphogenetic program. Two types of programs are possible. The first requires a feedback from the sculpture on earlier whorls, in order to arrange properly the sculptural elements on the current one. For this reason, we decided to call sculptural patterns of this type *synchronized*. The construction of sculptural elements on successive whorls is allochronous, rather than synchronous. However, the observed regularity of the sculpture suggests that, in a synchronized pattern, the trigger that initiates the construction of a new element is essentially simultaneous with, and caused by, the feedback signal from an earlier element. How this feedback can be obtained by the organism is discussed below.

An alternative type of program may trigger the construction of a new element, based on the ticking of an internal timer. In this case, the term "timer" should be intended in a broader sense than a time counter, since such a timer could be influenced by exogenous factors (*e.g.*, environmental parameters like temperature changes and tidal rhythm) as well as endogenous ones (*e.g.*, growth rate, availability of food, and endocrine activity). Such a program would follow a regular sequence in the construction of sculptural elements, albeit independently of earlier sculpture or other morphological characters of the shell.

In the absence of accidental disturbances, and assuming that the rate of shell growth does not change substantially during growth, patterns controlled by either type of mechanism can be expected to show a consistent reciprocal placement of sculptural elements. In this respect, both mechanisms may produce similar results. When "accidents" do occur, however, the two mechanisms may react in different ways. For instance, a temporary disturbance may cause a single sculptural element to be built in a wrong position. In the presence of a feedback from earlier sculpture (type 1 mechanism), the pattern may self-repair, so that the following elements are placed again in the correct positions.

In the absence of such feedback (type 2), or in the presence of a feedback exclusively between the current element and the immediately preceding one, the timer may recover its regularity afterwards, but the offset introduced by the disturbance with respect to earlier sculpture may remain constant, causing all subsequent sculptural elements to be arranged incorrectly with regard to elements built before the disturbance. This phenomenon may be compared to a set of two clocks. If the two clocks are initially synchronized, and one of the clocks' hands is subsequently moved by an external force, the two clocks afterwards remain offset by a constant amount of time with respect to each other.

This different behavior of the two types of morphogenetic program may allow their inference from observations on the morphology of actual gastropod shells, even if the synchronization mechanism itself is not studied directly. The second type of program may be termed *periodic*. This term is already in use, in a descriptive sense, to indicate patterns that alternate between different states during their construction. Thus, a periodic pattern may or may not be juxtaposed, and may also shift from one condition to the other during shell growth.

Synchronized sculpture, as defined above, usually does possess a visible juxtaposition, and its elements are usually collabral (*e.g.*, varices, collabral ribs, swellings and/or constrictions) or arranged in collabral series (*e.g.*, sets of spines built simultaneously along the perimeter of the aperture). Therefore, a search for synchronized sculpture in gastropods can be restricted to taxa possessing this distinctive type of sculpture.

The main practical problem, in this context, is deciding whether a given periodic sculpture is synchronized. In practice, the recognition of synchronized sculpture can be based on the existence of a fixed (or at least visibly consistent) arrangement of sculptural elements that causes elements on successive whorls to be aligned in one or more series running in an approximately antero-posterior direction. In some cases, elements are not aligned in a straight line, but rather in a slightly spiral fashion (*e.g.*, Fig. 7J) due to a small angular offset between elements on successive whorls. This is also easy to recognize from observation.

When a gastropod species exhibits the above characteristic, it can be examined more closely to determine whether the sculpture is truly synchronized. If the alignment of sculpture is consistent among individuals of the same species and along a significant number of whorls (ideally, all or most of the shell past the larval and juvenile stages), the identification of synchronous sculpture is reasonably certain. On the other hand, if the reciprocal position of sculptures on successive whorls deviates often from a regular pattern, the occurrence of synchronization may be questioned.

The number of sculptural elements per whorl can be used as a convenient short-hand notation to indicate the general type of patterns. Thus, base-2, base-3 and base-5 patterns possess 2, 3 or 5 sculptural elements per whorl, respectively. Small rotational offsets from one whorl to the next are ignored in this notation.

In a few cases, the number of elements per whorl is not an integer (and is not close enough to an integer to be rounded off). Consequently the base must be expressed as a fraction, like 3/2. A base-3/2 pattern has elements spaced 2/3 of a whorl from each other, yielding 3 elements (and their associated spacing) in a set of 2 complete, successive whorls. Such a pattern is common, for instance, in the Ranellidae (see below).

DESCRIPTIONS AND OBSERVATIONS

This section is arranged by family, since this level of resolution provides a suitably broad reference frame. The families are arranged in a sequence convenient for the present discussion. The adaptive significance of each sculptural type is best examined in a broader context in the subsequent section.

Only a few families of gastropods were examined in detail, as a cursory review of most families showed them to be of little or no relevance to this study. For instance, many families possess consistently smooth shells, or sculpture with a predominantly spiral arrangement (*e.g.*, the large majority of heterobranchs and non-marine gastropod families, as well as most taxa regarded as "archaeogastropods"). It is possible that isolated taxa within some of these families do possess a synchronized sculpture, and have been overlooked by us. Thus, the present study is far from being an exhaustive survey of the occurrence of synchronized sculpture in gastropods. This section also includes notes on a few instances of periodic sculpture that turned out not to be synchronized under detailed scrutiny.

Observations were also carried out on morphological characters that may yield clues to the nature of the morphogenetic phenomena controlling the construction of synchronized sculptures. The significance of these observations is discussed in the next section.

Eulimidae

Representatives are parasitic on echinoderms. An ectoparasitic eulimid is attached permanently or temporarily to its host by the proboscis. An endoparasite is buried partly or completely within its host. Most Eulimidae possess extremely smooth shells, lack any projecting sculpture, and are slippery to both potential predators and humans (Vermeij 1983, Warén 1983). In other gastropods, such as the Cypraeidae, Olividae, and Marginellidae, a slippery shell is probably adaptive in making it difficult for shell-peeling or shell-crushing predators to manipulate the shell (Vermeij 1983). This may be the case with the Eulimidae as well.

The typical shell geometry in this family is an acute cone, usually with a closed umbilicus and a rounded to oval shell aperture. A striking characteristic of several representatives is that the shell is bent about the coiling axis throughout its length (Fig. 1A-E). This condition is very unusual in gastropods, and deserves a detailed investigation. "Unmodified," straight shells are assumed to be the primitive condition (Warén 1983).

In all observed instances, curvature of the coiling axis is associated with the occurrence of a row of coarse growth lines aligned in an antero-posterior or slightly oblique direction along the concave side of the shell. Only one such growth line is present on each whorl, and likely marks a position at which shell growth stopped for some time before resuming. These lines were called incremental scars by Warén (1983). The shell is typically thickened inside in the region immediately preceding each incremental scar, for up to one quarter of a whorl. In translucent forms, this thickening often results in a visible "clouding" of the shell surface (Fig. 1C-D). This feature can be likened to an internal varix, but is not as distinct as a typical varix.

The fact that growth stops for a substantial time at each incremental scar, and apparently takes place at a rapid rate between successive scars, is indicated by the fact that we were unable to observe specimens collected while building the shell region between successive thickenings. Eulimids as a whole are relatively common, and abundant material of several species was available to us. An even growth rate should result in a sizable portion of specimens being captured while growing between incremental scars.

The periodic internal thickenings, and corresponding incremental scars, of curved eulimids constitute the only base-1 periodic sculpture studied in the present paper. We are not aware of similar patterns in other gastropods, except for a species of *Colubraria* Schumacher, 1817 mentioned below. Not all eulimids, however, display this pattern. Several forms, like *Niso terebellum* (Linnaeus, 1758) (Fig. 1F), normally do not display evident and repeated incremental scars, while others possess them, but distributed at irregular intervals, instead of aligned into a base-1 pattern. According to Warén (1983), some specimens of *Melanella martini* (A. Adams *in* Sowerby, 1855) have incremental scars synchronized in a base-1 pattern on most of the shell, while in other specimens the incremental scars are scattered. Finally, a few forms possess a base-2 sculpture pattern (Fig. 1N-P). All forms devoid of a base-1 pattern possess a straight coiling axis. However, a few straight forms also possess incremental scars aligned on one side of the shell, often fully comparable with the base-1 patterns of curved forms. It may be mentioned also that the subgenus *Pseudoretusa* Ponder and Gooding, 1978 has an involute shell comparable with that of the opisthobranch *Retusa* Brown, 1827, but (at least in the adult) markedly bent about the columella (cf. Warén 1983: fig. 177). This curvature may arise only in the last whorl or be "inherited" by the last whorl(s) enveloping a curved juvenile stage not dissimilar from

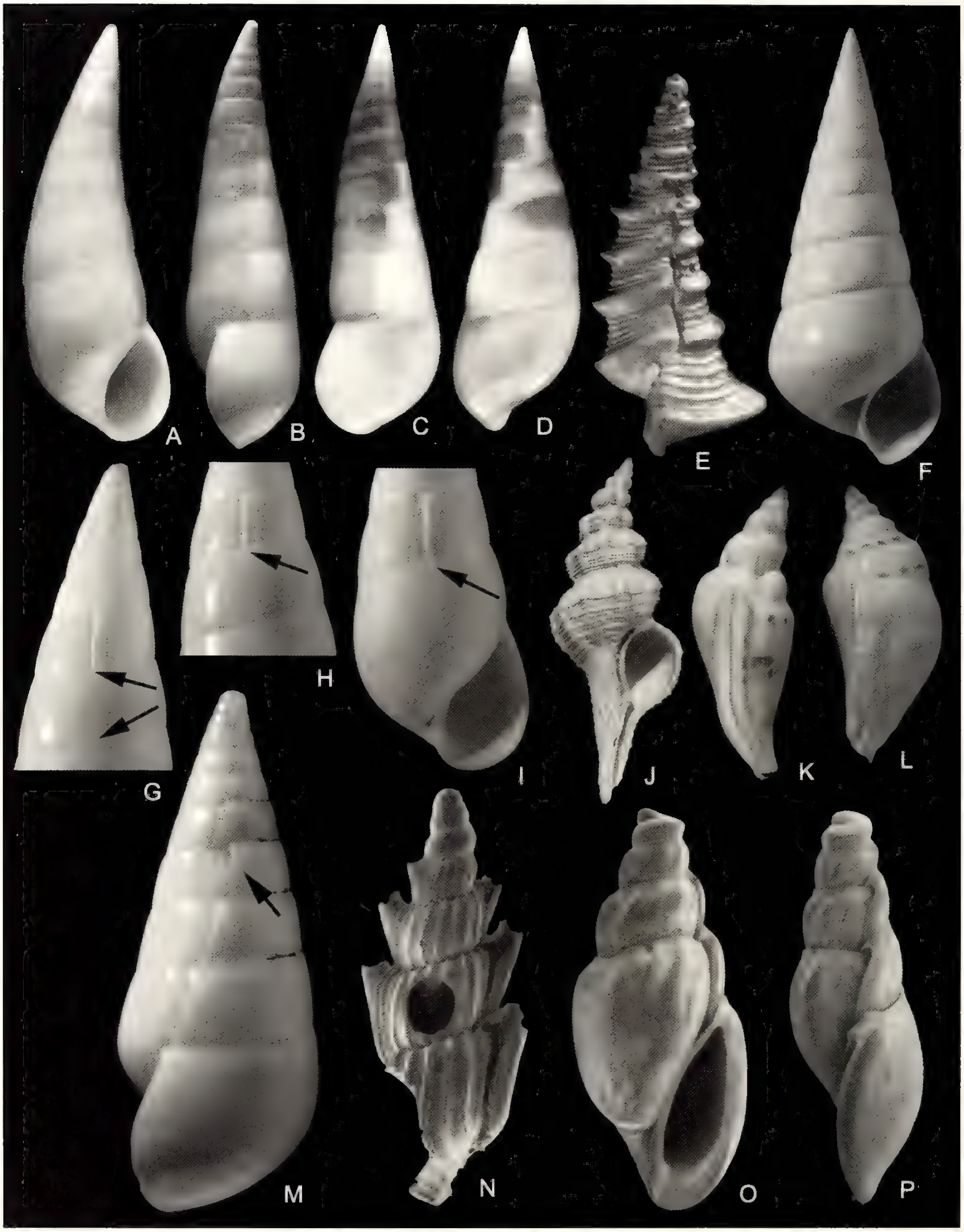

Figure 1. Eulimidae (except J-L). A-D. *Melanella* sp., Recent, Catarman, Cebu, the Philippines, shell lengths 19 mm (A-B), 18 mm (C-D) (ES). E. *Bacula striolata* H. and A. Adams, 1854, Recent, Pacific Ocean, 20 mm (Bordeaux Museum of Natural History) (photograph courtesy of A. Warén). F. *Niso terebellum*, Pliocene, Castell'Arquato, Italy, 23 mm. G-I. *Melanella cumingi* (A. Adams, 1854), Recent, Seychelles, 18 mm (SMNH). J. Abnormal specimen of *Fusinus* sp., Pliocene, Castell'Arquato, Italy, 42 mm (ES). K-L. Abnormal specimens of *Strombus mutabilis* Swainson, 1821, Recent, Cebu, the Philippines, 35 mm and 33 mm, respectively (ES). M. *Melanella martini* (A. Adams, 1854), NW Australia, 27 mm (SMNH). N. Unidentified eulimid, Recent, Pacific Ocean, 2.7 mm (photograph courtesy of A. Warén). O-P. *Auriculigerina* cf. *miranda* Dautzenberg, 1925, Recent, Azores, 2.9 mm (photograph courtesy of A. Warén).

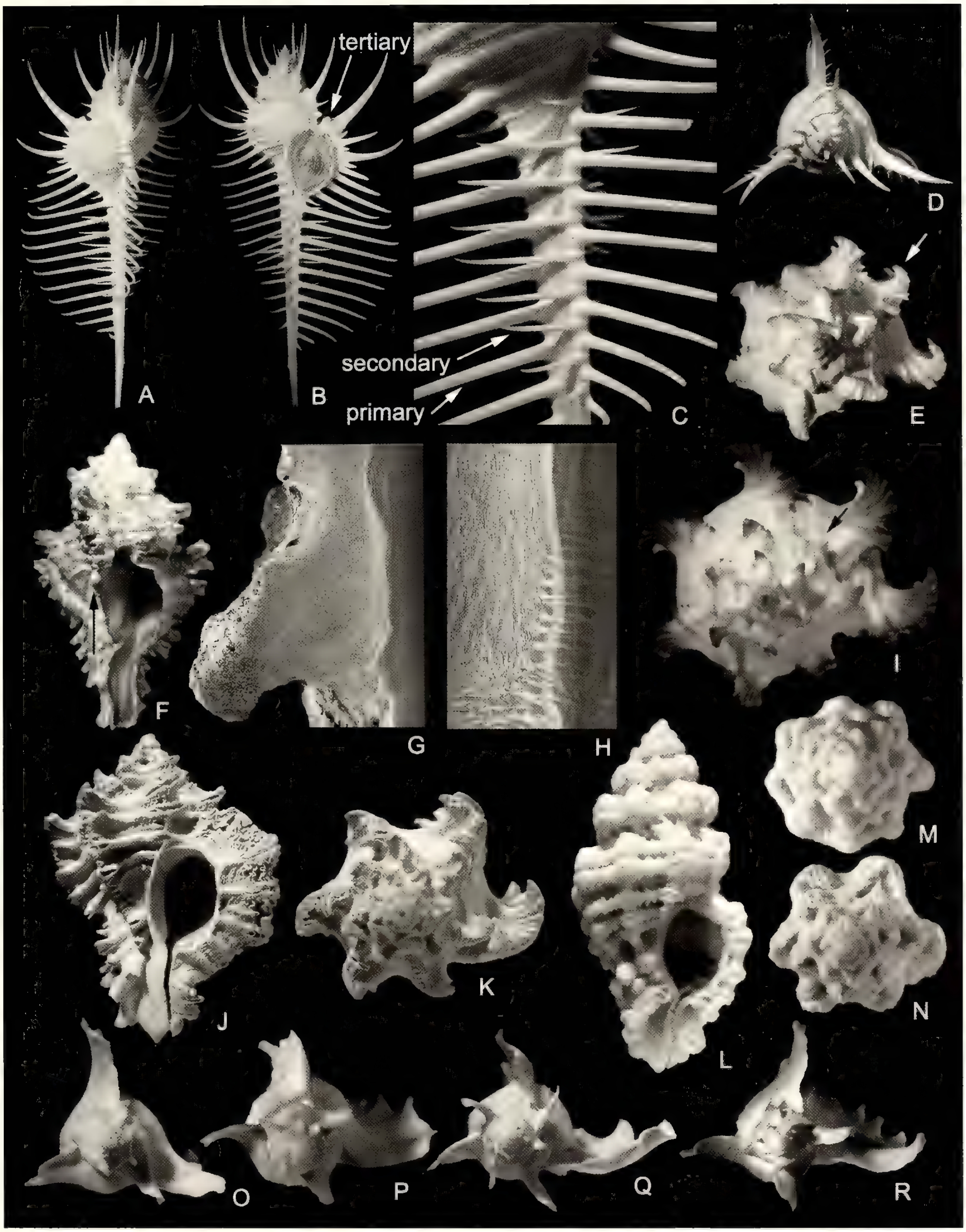

Figure 2. Muricidae. A-D. *Murex pecten*, Recent, unknown locality, 97 mm (SMNH). E, I. *Chicoreus chicoreum* (Gmelin), Recent, Cebu, Philippines, shell diameters 33 mm and 47 mm, respectively (ES). Specimen with misplaced varix (E, arrow) and specimen with broken and repaired varix (I, arrow). F-H. *Chicoreus brunneus* (Link), Recent, Tayud, Cebu, Philippines (ES). Specimen collected while building a growth increment (F, 27 mm), and details of spine on preceding whorl (arrow in F) being resorbed (G, field height 1 mm; H, field height 330 µm). J-K. *Murexiella absona* (Jan), Pliocene, Castell'Arquato, Italy, 16 mm (ES). L-M. *Ocenebra intermedia* Adams, Recent, Bermuda, 18 mm (ES). N. *Favartia cellulosa* (Conrad), Recent, Bermuda, shell diameter 9.5 mm (ES). O-R. *Pteropurpura adunca* (Sowerby, 1834), Ushibuka Fishery Port, Amakusa Islands, Japan, shell diameters approximately 35 mm (ES).

a curved *Melanella* Bowdich, 1822. Understanding the morphogenesis of this genus will require the examination of juvenile and subadult shells.

Muricidae

The life habits are highly differentiated among subfamilies, but rather invariable within subfamilies. They are carnivorous, usually drilling the shells of their prey by a combination of radular action and an accessory boring organ (Carriker 1981). This large and morphologically diverse family typically displays a sculpture pattern consisting of periodic varices. In most cases, muricids with a strong sculpture remove part of it from the surface of the earlier whorl before covering it with a new growth increment. This process has been observed in few species (see below), but likely takes place with little or no variation in most representatives of the family, since strong sculpture seems to have appeared and disappeared multiple times in separate genera, and its removal from the preceding whorl often is required to allow shell growth.

Shell growth in muricids takes place in spurts, or episodes, separated by an extended pause (see references below). Each episode of growth secretion starts with the relatively quick construction of a thin region of shell, followed by a new varix. Illert (1981) reported that the complete construction of a new growth stage (including a new apertural varix) in aquarium-kept *Pterynotus triformis* (Reeve, 1845) takes almost two months, and is followed by a pause of five months. This growth process is not as quick as the one described as episodic by Linsley and Javidpour (1980) in other gastropod families. McKenzie (1961) reported that the muricid *Eupleura caudata* (Say, 1822) builds a growth increment in about three weeks, and repeats this process once or twice a year.

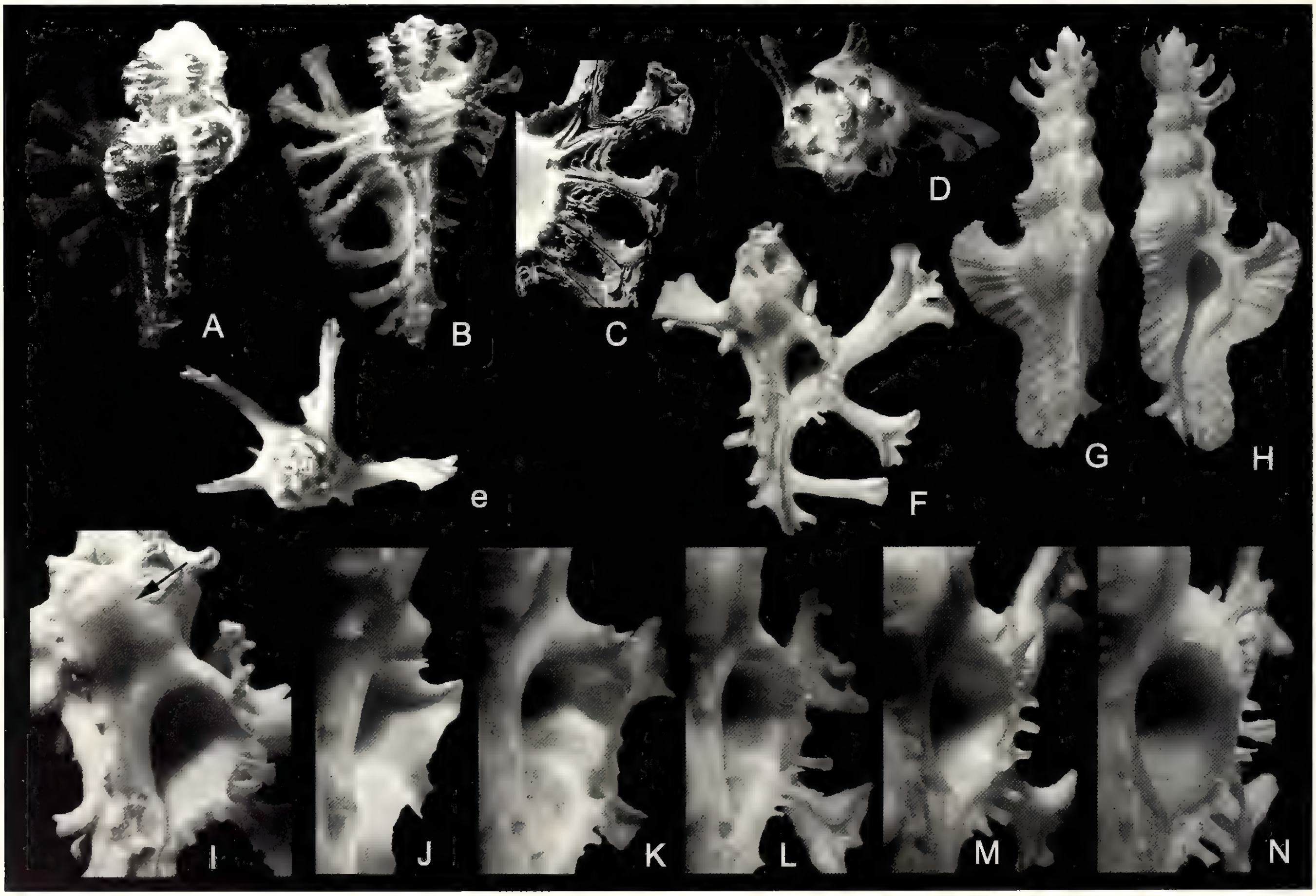

Figure 3. Muricidae, all Recent, Cebu, Philippines (ES). A-D. *Homalocantha scorpio.* Normal adult (A, 41 mm), unusual specimen with preserved spines (B-C, 45mm) and details of apertural spines in adoral view (D, shell diameter 32 mm). E-F, I-N. *Homalocantha zamboi.* Ventral (E, 58 mm) and apical (F) views of adult, detail of aperture, showing patch of secondary resorption of early spines (arrow in I, field height 23 mm), and growth series showing the successive stages of construction of apertural spines (J-N, field height 23 mm). G-H. *Pterynotus elongatus* (Lightfoot, 1789), 82 mm.

Spines accompanying a varix are built initially as hollow structures, and afterwards are thickened gradually by projections of the mantle that occupy their cavities and retract as the latter fill with shell material. Both the region located between successive varices and the last varix are thickened secondarily after being built. Morphologically complex varices or "wings" with their accessory structures require a correspondingly complex sequence of expansions and contractions of the mantle tissues, accompanied by substantial changes in their shape (*e.g.*, Figs. 2A-C, 3C, 5A-B).

When the behavior of muricids was observed during construction of a growth increment, it was found that the organism ceases feeding and seeks shelter during this process. Details of this process and/or its associated morphological and behavioral changes were discussed, for instance, by Abbott (1954), Inaba (1967), Linsley and Javidpour (1980), and Illert (1980a, 1981).

In muricids with strong varices, a new episode of shell growth requires the removal of part of a preceding varix and associated spines. Our observations are based on two specimens of *Chicoreus brunneus* (Link, 1807) collected while building a new growth increment (Fig. 2F-H). Both specimens had built a thin shell across most of the space between adjacent varices (judging from the length of similar intervals in previous growth episodes), but had not commenced the construction of the apertural varix. The mantle tissues had reached the position of the corresponding varix on the preceding whorl, and had commenced to resorb the basis of the spines in this region (Fig. 2F). SEM observations show the alternating first-order units of crossed-lamellar structure in the region of resorption. Its surface cuts through the crystallites as clearly as an artificially polished and etched section (leftmost portion of Fig. 2G-H). Simultaneously, or in a repeated alternation of phases, shell secretion takes place along the inner lip of the shell (rightmost portion of Fig. 2G-H). The shell surface in this region is smooth, or bears only a slight relief, at least in part corresponding to the crystallites of the underlying etched region. The spines are not resorbed in their entirety, but only along their bases. Presumably, they break off as bioclasts shortly thereafter. This process is essentially identical to that described by Carriker (1972) in *Chicoreus brevifrons* (Lamarck, 1822) and *Hexaplex fulvescens* (Sowerby, 1834).

Most muricids display an evident juxtaposition of sculptures. Accidental disturbances of these patterns are rare and generally restricted to an incorrect placement of isolated varices at or near the adult stage (*e.g.*, arrow in Fig. 2E). The pattern often regains its regularity after a varix is broken off and the shell repaired (arrow in Fig. 2I).

Base-3 (Fig. 2A-D) and base-5 patterns are very common in this family. Base-6 patterns (Fig. 2K, N) are also common. A higher number of varices per whorl usually results in a non-synchronized pattern (*e.g.*, Fig. 2L-M, Fig. 5A-B). Base-2 and base-4 patterns are rare, and are discussed below. Although synchronization is usually good (*i.e.*, specimens that deviate from these patterns are rare), species of *Pteropurpura* Jousseaume, 1880 and related genera may display a high intraspecific variability in the angular offset of varices between adjacent whorls (Fig. 2O-R). While the normal situation in this species is a base-3 pattern (Fig. 2O), extreme cases display a true base-4 pattern (Fig. 2R). Intermediate specimens may show either a constant or a changing amount of offset during growth (Fig. 2P and 2Q, respectively). The juvenile stages of several of these species possess several varices per whorl (often 7 or more), and usually no synchronization.

In *Murex pecten* Lightfoot, 1786 (Fig. 2A-D) and related species (see Ponder and Vokes 1988), the distinctive pattern of very long spines forms a protective canopy above the head and body of the mollusk (Paul 1981). These spines form distinct hierarchies (Paul 1981, Seilacher 1992). Fig. 2B-C shows the nomenclature introduced by Paul (1981). The terms primary, secondary and tertiary are meant to be descriptive, refer to the size and direction of the spines, and do not indicate an ontogenetic or morphogenetic sequence (in fact, all hierarchies of spines on the same varix probably are built roughly at the same time). Secondary and tertiary spines generally cover areas left unprotected by primary spines. Shell growth in these muricids requires the removal of most of the spines on the second-to-last growth increment

Homalocantha scorpio (Linnaeus, 1758) (Fig. 3A-D) possesses large, T-shaped or club-shaped apertural spines on the last varix. As inferred from growth lines and individuals collected at different growth stages, the spines are built by a complex process, in which the mantle retracts several times toward the aperture. This leaves a set of distinctive ridges, marking the successive positions of the mantle (Fig. 3C).

Homalocantha scorpio builds a set of spines along each varix, but earlier spines break off or are worn away quickly, usually leaving only the last set of spines. It seems unlikely that the apertural spines are partly resorbed prior to each growth increment, because there is no visible trace of secondary resorption on earlier spines, so their disappearance is likely due to mechanical wear. This may be favored by the fact that earlier spines point in an obliquely dorsal direction and are therefore exposed, while the last set of spines lies flat against the substrate. In occasional individuals, the spines are not broken off, or break off gradually, leaving two or more sets (Fig. 3D). Such specimens often show a well-preserved shell surface, while typical specimens may be considerably corroded. Thus, these spine-bearing individuals may come from low-energy or otherwise sheltered environments. This further supports the idea that mechanical wear is the main factor involved in the removal of the spines. Several species of *Homalocantha* with lesser-developed spines show only a minor wear of earlier spines during shell growth.

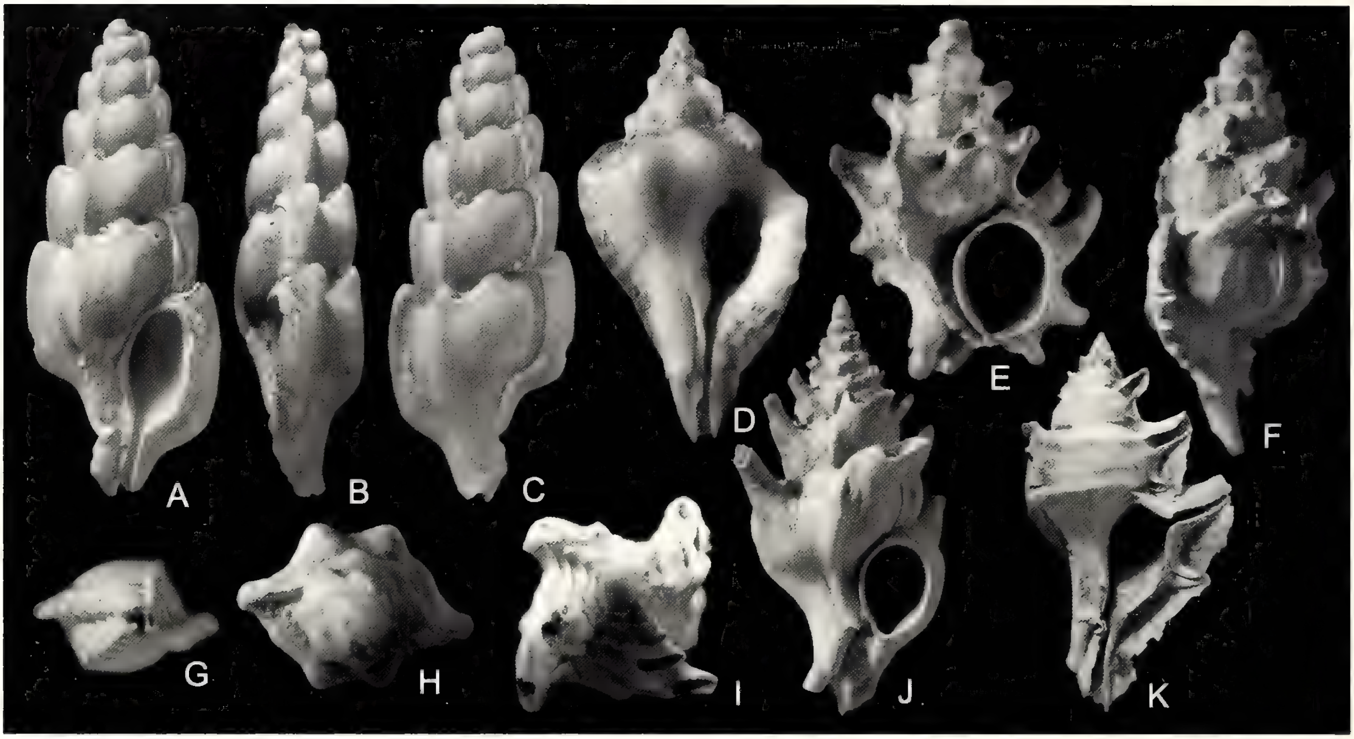

Figure 4. Muricidae. A-C, G. *Aspella* sp., Recent, Tayud, Cebu, the Philippines, 16.5 mm (ES). D, H. *Eupleura caudata*, Recent, Florida, USA, 24.5 mm (ES). E. *Typhis horridus* (Brocchi), Pliocene, Siena, Italy, 15.3 mm (ES). F. *Typhis* (s.l.) *tubifer*, Eocene, Grignon, Paris Basin, France, 22 mm (ES). I-J. *Typhis fistulosus* (Brocchi, 1814), Pliocene, Tabiano Terme, Italy, 13.5 mm (ES). K. "*Pterynotus*" *bispinosus* (possibly a Prototyphis), Barton Beds, Barton, UK, 24.5 mm (CU, C59298).

Homalocantha anatomica (Perry, 1811), *H. zamboi* Burch and Burch, 1960 (Fig. 3E-F, I-N) and *H. anomaliae* Kosuge, 1979 possess fewer and longer spines than *H. scorpio*, and these spines normally do not break (however, Vermeij [1983: fig. 2.10], illustrated a specimen of *H. anatomica* with completely eroded spines on two varices preceding the last one). These species invariably show a broad patch of secondary shell resorption extending from the aperture onto the ventral region of the preceding whorl (Fig. 3I). All spines in this region are resorbed, presumably by a process similar to the one observed in *Chicoreus* Montfort, 1810 (see above).

A growth series in *Homalocantha zamboi* (Fig. 3J-N) shows the distinct phases of construction of the apertural spines. The major spines are initially built as hollow, fluted structures that become thickened gradually (Fig. 3J-Ll). While and after the major spines are filled with shell material, the mantle builds a second set of smaller spines around the outer lip (Fig. 3L-M), and finally a sharp apertural rim within the second set of spines (Fig. 3N).

The varices in *Homalocantha scorpio* are not synchronized, while those in *H. zamboi* (and presumably similar species) show a consistent juxtaposition to those on earlier whorls. In *H. zamboi*, a well-developed foil-like expanse of shell material bridges each varix with the preceding whorl across the whorl suture. Thus, the mantle tissues at this stage were in direct contact with the sculpture of the preceding whorl. *H. zamboi* possesses a base-5 pattern (allowing for a relatively large offset between the varices on adjacent whorls; Fig. 3E), in which the spine in the ventral position is secondarily resorbed, thus giving the impression of a lopsided base-4 pattern. *H. scorpio* possesses from 5 to 7 varices per whorl.

The Typhinae are characterized by periodic varices, visibly synchronized, and by a posterior tube communicating with the internal shell cavity, presumably with an excurrent function, located near the aperture and pointing in a posterior or postero-dorsal direction. Each varix is associated with one such tube, but only the last tube opens within the shell cavity. All others are sealed at their bases. Some Typhinae live within algal mats covering hard substrates (A. Warén pers. comm.), while other are recorded from sandy bottoms (*e.g.*, Higo *et al.*,1999). The characteristic tube may be associated, in general, with a life habit that is semi-infaunal in sediment, and/or embedded in an algal substrate.

Within this subfamily, there is a considerable diversity of morphology in the length and placement of the tubes. In most species of *Typhis s.s.*, *Typhina* Jousseaume, 1880, *Typhisala* Jousseaume, 1880, *Typhisopsis* Jousseaume, 1880, *Haustellotyphis* Jousseaume, 1880, *Siphonochelus* Jousseaume, 1880, and *Trypterotyphis* Jousseaume, 1880, tubes are located approximately midway between successive varices (Fig. 4E-F). In the Neogene to Recent *Typhis sowerbyi* (Broderip, 1833), which represents an extreme case, the tubes are significantly closer to the preceding varix than to the following one. In *Pterotyphis* Jousseaume, 1880 and a few species of *Typhis* Montfort, 1810 (Fig. 4J), tubes are located very close to the following varix. Paleogene Typhinae often display a base-4 pattern (Fig. 4I), otherwise very unusual in muricids. In forms that alternate varices and tubes at roughly equal spacing, this pattern is less evident, and further masked by a large amount of angular offset between successive whorls. Base-3 patterns seem to be more frequent among Recent forms, although base-4 patterns still occur. A further difference among fossil and Recent representatives is that the varices seem to be more developed in Recent forms, where often they take the shape of expanded apertural wings, while fossil forms typically possess sets of isolated spines or massive, scarcely projecting varices. The size of Recent Typhinae is also generally larger than in Tertiary fossils.

Trubatsa Dall, 1889 (*e.g.*, see Abbott and Dance 1983: 157) possesses a very long posterior last tube and an equally long anterior siphonal tube. Each tube may exceed the length of the coiled portion of the shell, and both tubes point in an obliquely dorsal direction. Apparently, the tubes are optimized as siphons, with the anterior one being the incurrent. Both tubes are resorbed or broken off in earlier growth stages. Since we have no material available of this interesting genus, we are unable to discuss in detail its shell construction and functional morphology. However, similar (albeit shorter) tubes are present, for instance, in the Eocene "*Typhis*" *tubifer* Bruguière, 1792 (Fig. 4F), in which they seem to wear off gradually. A very long anterior siphon is present also in a few species of *Murexiella* Clench and Pérez Farfante, 1945 (Fig. 5B), in which it breaks off gradually during subsequent growth stages. No secondary resorption seems to be involved in either example.

Prototyphis Ponder, 1972 deviates from this pattern in that there is no separate tube, but instead a large spine located on the varix remains open along its entire length and forms a deep furrow that communicates with the inside of the shell aperture. The Eocene "*Pterynotus*" *bispinosus* (J. de C. Sowerby, 1823) (Fig. 4K) possibly belongs in this genus. The spines in true *Pterynotus* are always filled with shell material, and/or sealed at their bases, while in this species the furrow within the major spine on the apertural varix always communicates with the shell cavity. When other spines are present along the aperture, they are gradually filled with shell material like typical muricid spines. *Prototyphis* differs from typical Tertiary Typhinae also in its base-3 pattern.

It is uncertain whether *Prototyphis* represents an ancestral morphological stage in the evolution of the typhine tube, since the latter displays several differences in morphology and ontogeny. For instance, the typical typhine tube is always separate from the shell aperture, and often located at a significant distance from it. This optimizes it for reaching the surface of the algal mat. In addition, the hollow spine in *Prototyphis* always remains open along its ventral side, while the typhine tube is closed off from the aperture early in its construction. Spines superficially similar to those of *Prototyphis* are present in the Trophoninae (*e.g.*, *Calcitrapessa* Berry, 1959), but they are always sealed off at their bases shortly after construction, and therefore cannot function as siphons.

A few muricids display a base-2 pattern. Among these are *Aspella* spp. (Fig. 4A-C, G) and *Eupleura caudata* (Fig. 4D, H). *Phyllocoma* Tapparone-Canefri, 1881 also possesses a base-2 pattern (*e.g.*, see Abbott and Dance, 1983, p. 149), but with a considerable amount of angular offset (approximately 60° per whorl), which makes the pattern spiral quickly around the spire. Unlike the preceding instances, *Phyllocoma* does not display a subdued axial sculptures intercalated with the varices.

True base-4 patterns in muricids seem to be even less frequent than base-2 patterns. According to Cernohorsky (1967), *Favartia* Josseaume, 1880 is characterized by a base-4 pattern. In the same paper, he further discussed two Recent species of this genus as having such a pattern. However, as discussed above, base-4 patterns are frequent in the Typhinae.

Coralliophilidae (or Muricidae, Coralliophilinae according to recent studies)

These are ectoparasites on cnidarians, sometimes endolithic within the skeleton of the host but not embedded within its tissues. The radula is absent; they probably feed on the tissues and/or body fluids of their hosts. Several epifaunal representatives of this family possess strong sculpture. This is especially true of small-sized taxa like *Babelomurex* Coen, 1922 (Fig. 5C-H; see also Kosuge and Suzuki 1985), in which the long spines may increase the total shell diameter by four times the actual diameter of the shell whorls. Among these forms, synchronization of the sculpture on successive whorls seems to be the rule (Fig. 5C, E, G), although the amount of angular offset from one whorl to the next can vary (see especially Fig. 5E). Base-6 and base-7 patterns are the most frequent in these forms. On the other hand, *Latiaxis* Swainson, 1840 and related genera lack synchronization. This difference is explained in the following section.

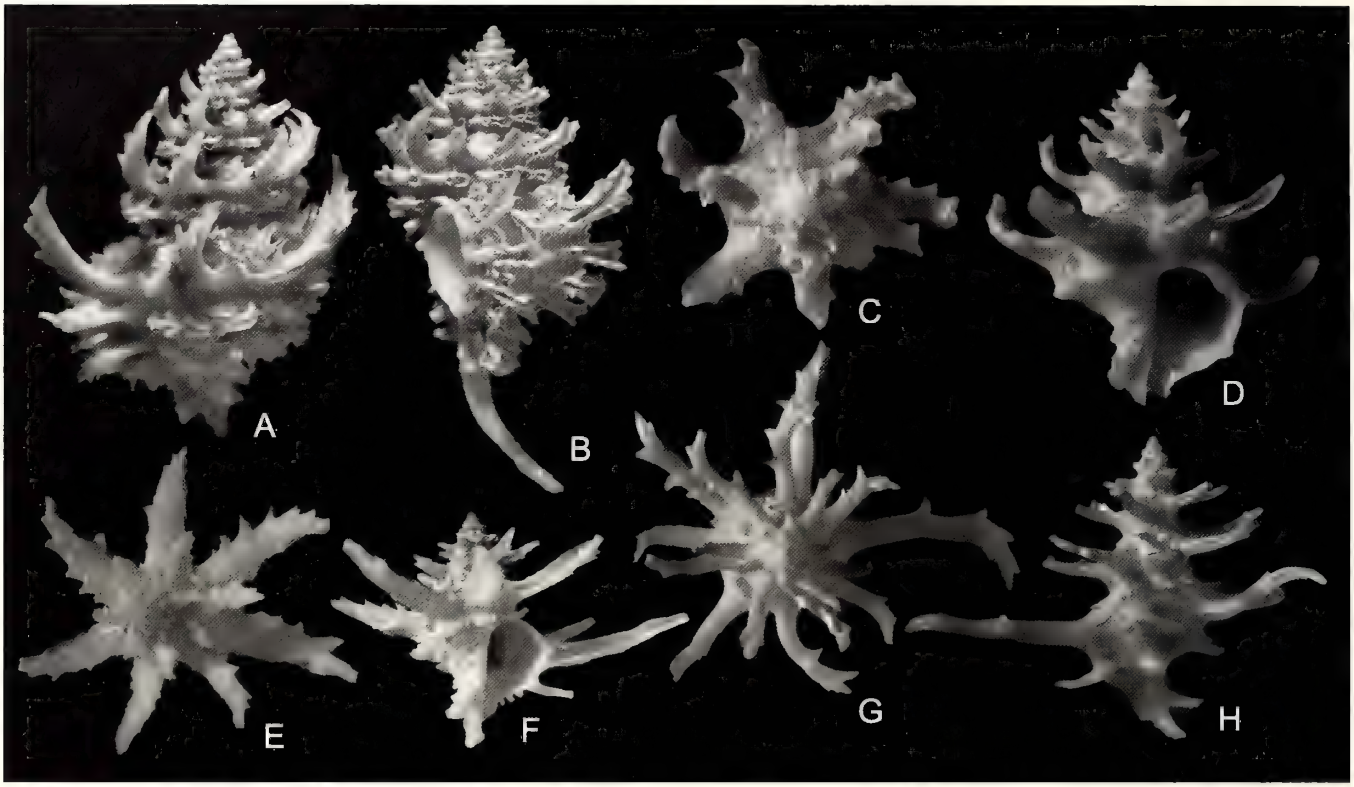

Figure 5. Muricidae (A-B) and Coralliophilidae (C-H), all Recent, Sogod Island, Philippines (ES). A. Murexiella judithae (D'Attilio and Bertsch, 1980), 16.3 mm. B. Murexiella pelepili (D'Attilio and Bertsch, 1980), 10.3 mm. C-D. Babelomurex cristatus (Kosuge, 1979), 11 mm. E-F. Babelomurex spinosus (Hirase, 1908), 7.5 mm. G-H. Babelomurex fruticosus (Kosuge, 1979), 13 mm.

Bursidae

The Bursidae are, at least in part, predators on polychaetes and sipunculids (Houbrick and Fretter 1969). Members of this family are characteristically epifaunal on solid substrates in shallow water, and often live in high-energy environments. The last varix carries a posterior excurrent canal (Fig. 6E-G), sometimes modified into a projecting spine (Fig. 6A-B). In *Bufonaria nobilis* (Reeve, 1844) (Fig. 6C-E, H-I) and *Crossata* sp., the shell bears a distinctive base-2 pattern of thickened varices. *Tutufa* sp. has a base-3/2 pattern with varices spaced approximately 240°, and different species of *Bursa* have either pattern (*e.g.*, see Beu 1998 and Cossignani 1994).

Bufonaria nobilis combines a base-2 pattern with determinate growth. On the dorsal region of the last whorl, sculpture becomes distinctly coarser (Fig. 6C, H). Morphs of this species develop the most central of the tubercles in this region into one or two large knobs (Fig. 6D-E, I). These changes sometimes affect a total of two or three half-whorls preceding the last varix, rather than the last half-whorl only (Fig. 6E, I). Comparable morphs may occur in other species.

Neogene representatives of *Bufonaria (Aspa) marginata* (Gmelin, 1791) (Fig. 6F-G) are unusually smooth for this family. The base-2 varix pattern and broad posterior siphon are typical for representatives of the family, but other characters, like the poor clamping geometry of the aperture (which can be observed by placing the shell on a flat surface), suggest that the life habits of this species may have been different from those typical of the Bursidae. Recent representatives of this species possess a significantly stronger sculpture, more typical for the family.

The Neogene to Recent *Bursa bufo* (Bruguière, 1792) (see Jung 1969: pl. 49, fig. 5-6) is particularly flattened dorso-ventrally in large adults, in which the width/dorso-ventral thickness ratio (including the varices, which are not especially projecting) is 1.6.

Ranellidae (=Cymatiidae) and Personidae

These are epifaunal, predatory gastropods mainly found on rocky substrates. Most feed on echinoderms (asteroids or echinoids) and molluscs (Day 1969, Houbrick and Fretter 1969, Laxton 1971). They display either a base-3/2 (Fig. 7A-E) or a base-2 pattern of thick varices (Fig. 7F-J) (Beu 1998). In a few instances (*e.g.*, the genus *Linatella* Gray, 1857), the base-3/2 pattern consists of just two successive varices in the

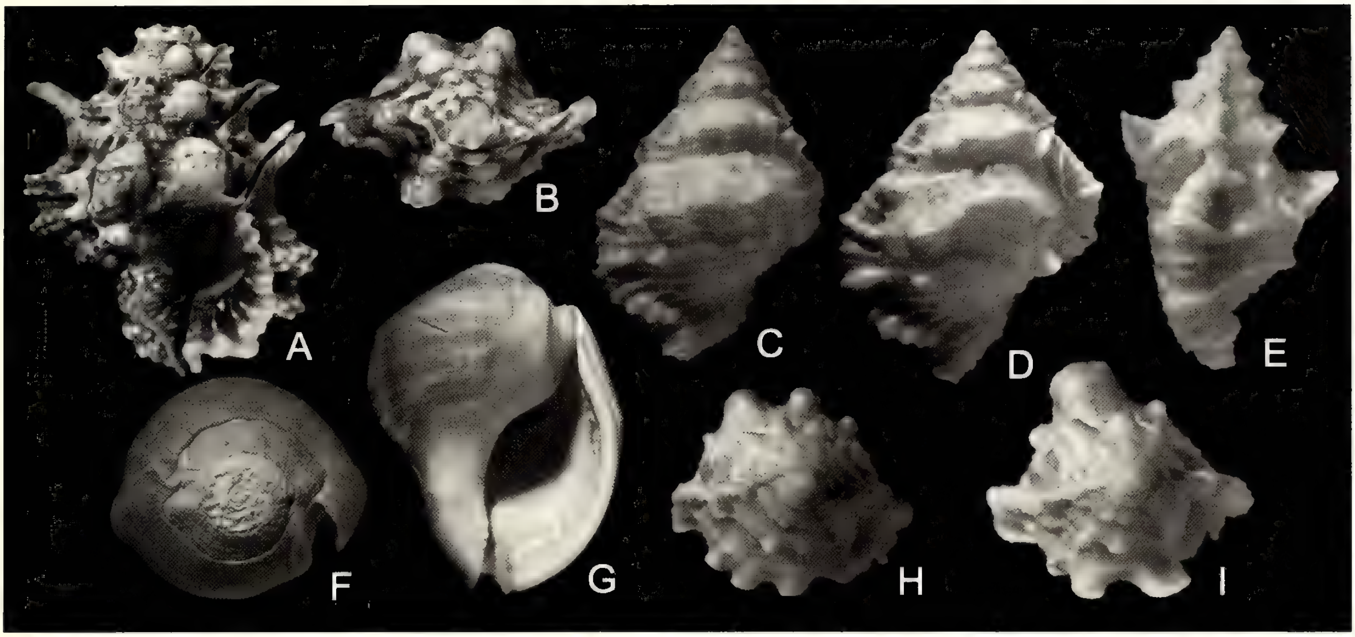

Figure 6. Bursidae. A-B. *Bursa lamarckii* (Deshayes, 1853), Recent, Cebu, Philippines, 66 mm (ES). C-E, H-I. *Bufonaria nobilis*, Recent, Cebu, Philippines, approximately 37 mm (ES). F-G. *Bufonaria (Aspa) marginata*, Pliocene, Castell'Arquato, Italy, 36 mm (ES).

adult shell region, while the rest of the shell carries only a spiral sculpture.

The shell regions located between successive varices typically bear knobs, tubercles, or other axial and spiral sculpture (Figs. 7-8). Together with the varices, these sculptures, especially in shells possessing a base-3/2 pattern, contribute to give a roughly triangular profile to the last whorl, as seen from the axial direction. In the genus *Distorsio* Röding, 1798, this effect is enhanced by the spire, which deviates from a regular spiral development between varices. In this genus, the callus covering the inner lip of the aperture has a very variable extension (Fig. 8A, D, F). In *Distortio reticulata* (Röding, 1758), a patch on the posterior region of this callus clearly replicates and reinforces the sculpture of the preceding whorl (Fig. 8G-K). Although the exact placement and size of this patch varies from individual to individual, it is always thicker, building massive knobs when fully developed, in correspondence of underlying original relief of the preceding whorl. In Fig. 8K, the sculpture on the preceding whorl is distorted by repaired shell damage, and the callus faithfully replicates this distortion. The oblique, elongated ridge visible in all illustrations below and to the right of the reinforced sculpture originates well within the shell aperture, apparently corresponding to a spiral ridge on the surface of the preceding whorl, thus representing another instance of sculpture triggered by an earlier relief, and only subsequently develops in an oblique direction, discordant from the underlying relief. Other species of *Distorsio* show a similar patch in the same region, albeit less evident than in *D. reticulata*. Other regions of the callus do not show this pattern, and are uniformly thickened (*e.g.*, Fig. 8A, D).

The sculpture pattern in *Distorsio* shows rather frequent instances of recovery from damage-induced irregularities. For instance, the specimen in Fig. 8E-F had most of the last growth increment peeled away by a predator, and regenerated it correctly (except for a small offset forced by the presence of part of the broken original varix in the posterior region of the aperture).

In *Gyrineum* (*Biplex*) spp., which possesses extremely developed varices (Fig. 7F-J), the portion of the whorl between varices is visibly flattened (Fig. 7F), yielding an elliptical cross-section of the whorl. Within the same species, some individuals further enhance the flattening by building a subdued sculpture in the central portion of the flattened regions (Fig. 7H). Interestingly, this morph recurs in distinct species of *Biplex* Perry, 1811. In *Gyrineum* (*s.s.*) and, to a lesser extent, in *Gyrineum* (*Biplex*), the varices are located at slightly less than 180° from each other, thus causing the pattern to spiral around the shell (Fig. 7F, J).

Buccinidae, Colubrariinae

Members of this subfamily are characteristic of hard bottoms, and hide under rocks during the daytime. Feeding is highly specialized; a long tubular proboscis sucks blood from sleeping fish at night (Johnson *et al.* 1995).

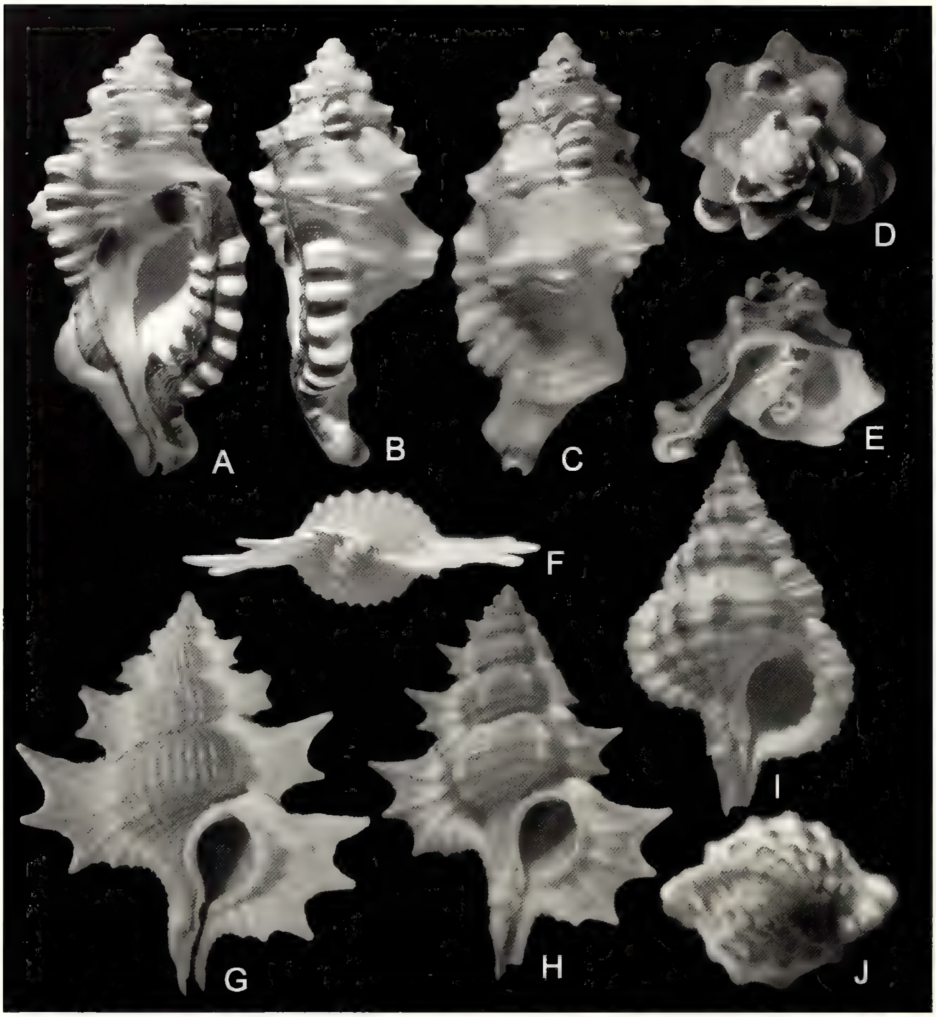

Figure 7. Recent Ranellidae, all from Cebu, Philippines (ES). A-E. *Cymatium lotorium* (Linnaeus, 1758), 83 mm. (E) shows a section through the last whorl, with a varix on the preceding whorl projecting into the shell cavity. F-H. *Gyrineum perca* (Perry, 1811), 44 mm. I-J *Gyrineum bituberculare* (Lamarck, 1816), 40 mm.

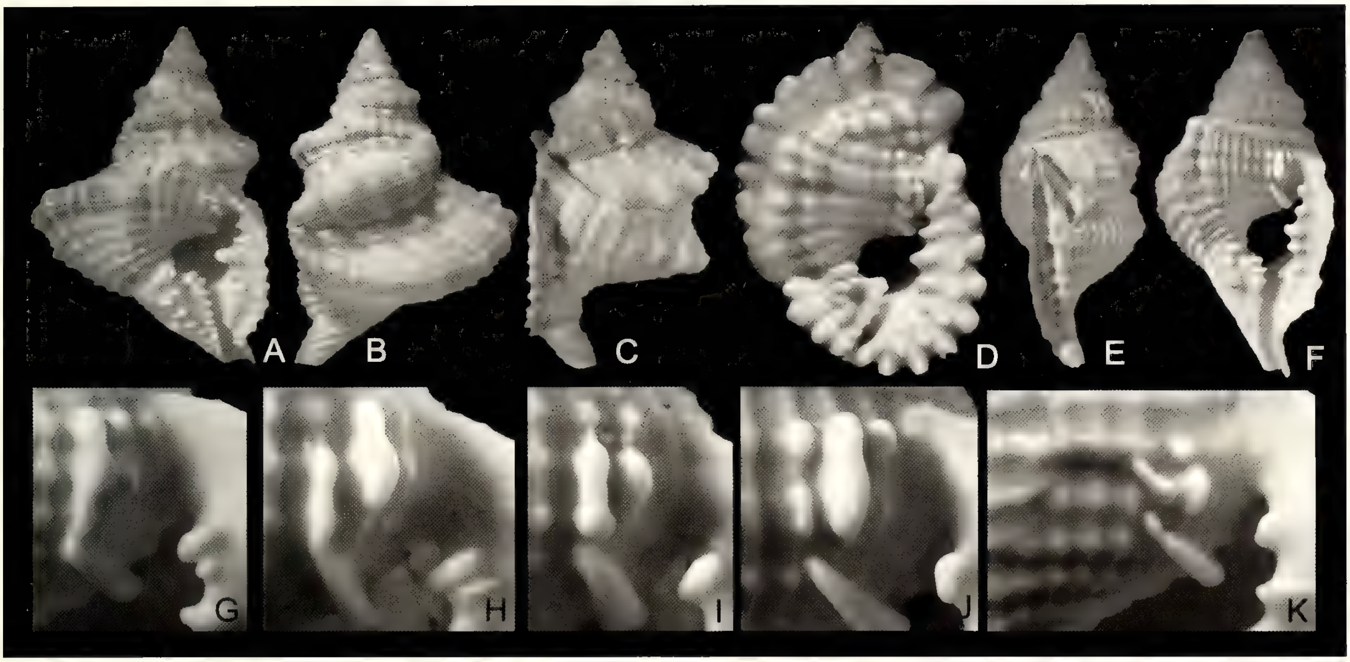

Figure 8. Recent Ranellidae or Personidae, all Recent from Cebu, Philippines (ES). A-C. *Distorsio kurzi* (Petuch and Harasewych, 1980), 37 mm. D. *Distorsio anus* (Linnaeus, 1758), 66 mm. E-K. *Distorsio reticulata* (Röding, 1798), 55 mm (E-F) and field heights 11 mm (G-K).

Members of this subfamily possess shells that are more slender than those of the Ranellidae and consist of a larger number of whorls. Most species display a base-3/2 pattern similar to that of the Ranellidae. A few species (*e.g.*, *Colubraria soverbii* (Reeve, 1844) and two unidentified species of *Colubraria* Schumacher, 1817 illustrated by Springsteen and Leobrera (1986: pl. 34, figs. 14 and 17), however, possess varices spaced slightly less than 1 whorl apart, thus spiraling rapidly around the whorl and not constituting a proper base-1 pattern. The angular interval between varices varies between approximately 270° and 330° in different species, and remains approximately constant in each individual, thus suggesting a synchronization.

Colubraria tortuosa (Reeve, 1844) (Abbott and Dance 1983: 173) apparently possesses a base-1 pattern of synchronized varices. As in representatives of the Eulimidae, the spire is bent (or more properly, exhibits a corkscrew-like twist).

Cassidae

These gastropods are found on sandy bottoms, mainly in the shallow subtidal zone. They feed by drilling echinoids (Lyman 1937, Abbott 1968, Illert 1980b, Hughes and Hughes 1987, Nebelsick and Kowalewski 1999). This family shows two main sculpture patterns (Abbott 1968, Kreipl 1997). The most common is probably a determinate growth pattern, in which a single thickened varix ends the growth process. The second type is a base-3/2 pattern, with varices spaced approximately 120° from each other (see above references). *Phalium areola* (Linnaeus, 1758) (Fig. 9L-M) and *Cassis cornuta* (Linnaeus, 1758) (Fig. 9N) are typical of this pattern. However, a few exceptions do exist. For instance, *Phalium decussatum* (Linnaeus, 1758) and *P. fimbria* (Gmelin, 1791) (Fig. 9K) display a base-2 pattern comparable with that of the Bursidae and part of the Ranellidae (see above). In all observed instances of base-3/2 and base-2 patterns in this family, a broad callus extends from the inner lip to touch and partly cover the preceding varix (Fig. 9L-N). Specimens with extra varices and/or varices placed at incorrect positions seem to occur relatively frequently in this family (*e.g.*, see Abbott 1968: pl. 8, fig. 10; pl. 14, fig. 7; pl. 64; pl. 75, fig. 4; pls. 85 and 114). The varices in this family are used to push away the spines of echinoids being predated upon (Lyman 1937, Hughes and Hughes 1987, Illert, 1980b), although this is probably not their only function.

Cerithioidea

Members of this superfamily are mostly epifaunal on or semi-infaunal or infaunal in soft bottoms in marine to freshwater environments. They are highly diversified in the tropical and subtropical zones, and are algal grazers or detritus feeders.

Several cerithiids, procerithiids, potamidids, and melaniids display a periodic sculpture consisting of stout spines or strong nodes. Often, the side of the whorl possesses several

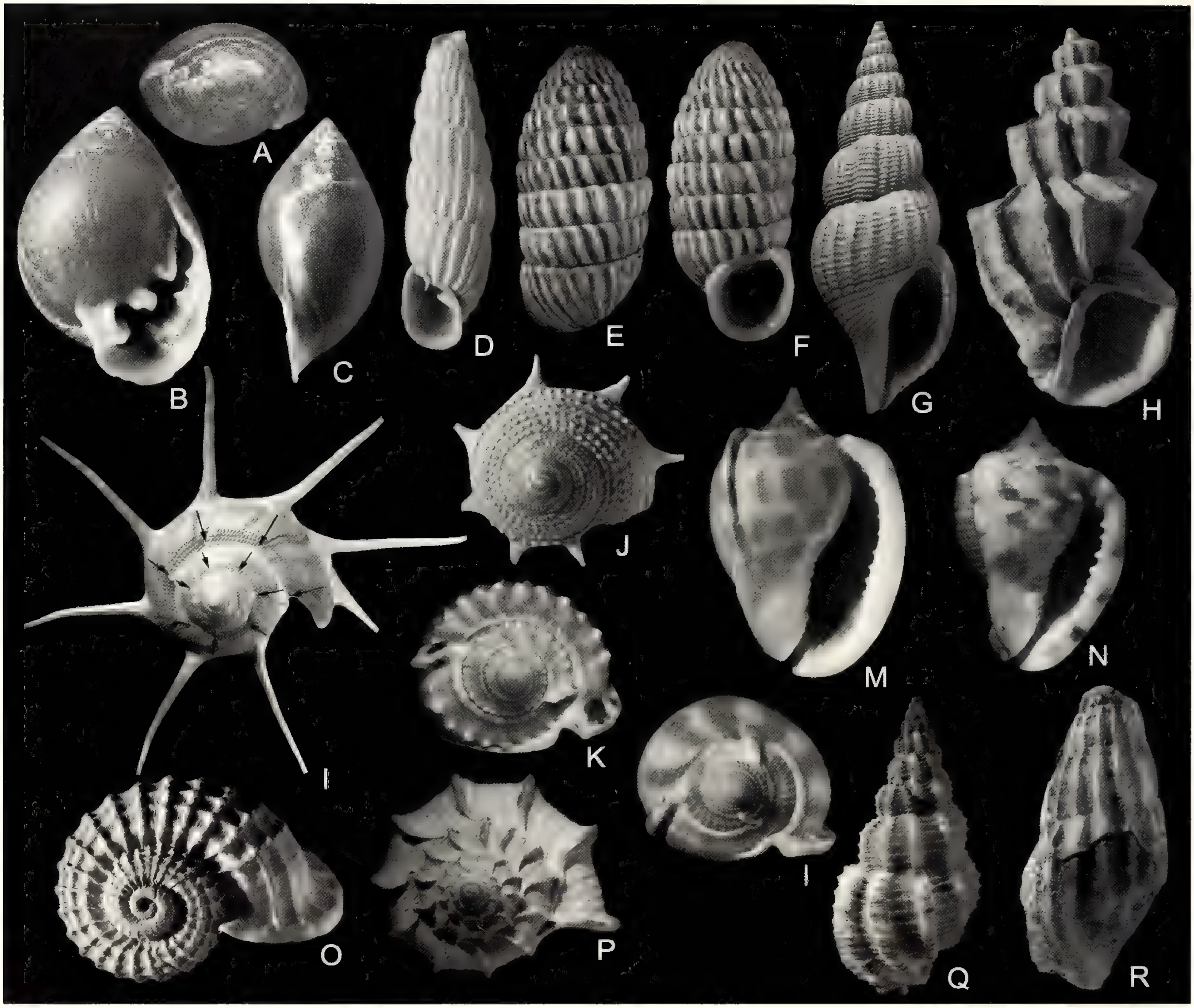

Figure 9. A-C. *Pythia scarabaeus* (Linnaeus, 1758), Recent, Tayud, Cebu, Philippines, 17.2 mm (ES). D. *Luchuphaedusa inclyta* (Pilsbry, 1908), Recent, Nakijin, Okinawa, Japan, 24 mm (NSMT). E-F. *Cerion uva* (Linnaeus, 1758), unknown locality (Caribbean), 22.5 mm (ES). G. *Rimella rimosa* (Solander, 1766), Middle Barton Beds, Barton, UK, 19.7 mm (CU, C58534). H. *Sveltia calcarata* (Brocchi, 1814), Pliocene, Castell'Arquato, Italy, 22.8 mm (ES). I. *Guilfordia yoka*, Recent, Cebu, Philippines, shell diameter (including spines) 81 mm (ES). J. *Guilfordia aculeata*, Recent, Cebu, Philippines, shell diameter 41 mm (ES). K. *Phalium fimbria* (Gmelin, 1791), Sri Lanka, 36 mm (CPM, ZM191) L-M. *Phalium areola* (Linnaeus, 1758), Recent, Cebu, Philippines, x1.2 (ES). Posterior (L) and apertural (M) views. N. Juvenile *Cassis cornuta*, Recent, Cebu, Philippines, 32 mm (ES). O. *Liotia warni* Cossman, 1902, Defrance, Eocene, Cotentin, France, shell diameter 16.4 mm (CU). P. *Eocithara mutica* (Lamarck, 1803), Middle Eocene, Chaussy, Paris Basin, France, shell diameter 36 mm (NHM). Q. *Phos senticosus* (Linnaeus, 1758), Recent, unknown locality (Indo-Pacific), 40 mm (ES). R. *Ectinochilus canalis*, Eocene, Cava Albanello, Vicenza, Italy, shell height of incomplete specimen 30 mm (ES).

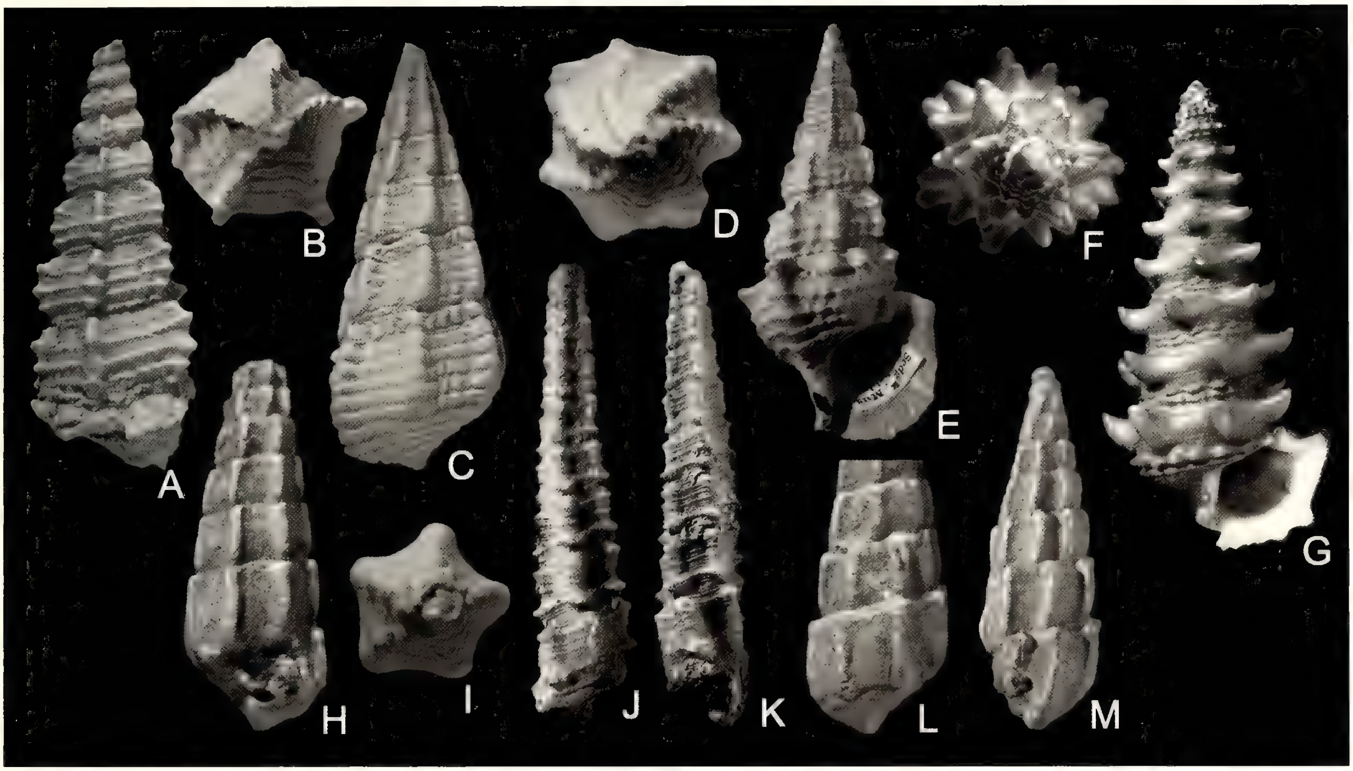

Figure 10. Cerithioidea (with the possible exception of I). A-B. *Pyrazus pentagonatus*, Eocene, Roncá, Italy, 37 mm (ES). C-D. *Pyrazus* cf. *vulcanicus* (Schlotheim, 1820), Eocene, Roncá, Italy, 39 mm (ES). E. *Pyrazus pentagonatus*, Eocene, Barton Beds, Barton, UK, 44 mm (CU). F-G. *Tympanotonos fuscatus* (Linnaeus, 1758), Recent, West Africa, 61 mm (UMUT). H, L-M. *Rhabdocolpus scalariformis* (Deslongchamps, 1824), Bajocian, Bayeux, Calvados, France, 28 mm (NHM, n. 81440). I. Undetermined cerithiid or turrid, Eocene, Roncá, Italy, shell diameter 7.5 mm (ES). J-K. *Cryptaulax contorta* (Deslongchamps, 1824), Jurassic, Les Moutiers, Bayeux, Calvados, France, 30 mm (NHM n. 81454).

spiral series of these sculptural elements. Sometimes, stronger and more broadly spaced elements are intercalated with smaller ones (*e.g.*, Fig. 10A-D, I). Strong sculptures of this type sometimes seem to be juxtaposed, thus suggesting a synchronization. However, a careful examination often shows that this ordering is disrupted frequently (Fig. 10H, L-M). Thus, this is not a true synchronization, but probably the result of sculptural elements being built at approximately constant intervals of time, accompanied by a roughly constant rate of shell growth.

Fig. 10J-K shows a particularly interesting instance. In this Mesozoic procerithiid, the angular offset between sculptures on successive whorls varies among individuals of the same species, and often within the same individual. As a result, the juxtaposition of sculpture sometimes follows an antero-posterior direction and other times a spiraling pattern around the shell. However, the inclination of the individual sculptural elements follows the overall inclination of the pattern: axial ribs are present where the pattern is aligned axially, and prosocline ribs where the pattern spirals around the shell. The pattern always follows the inclination of individual ribs, and this provides a strong indication of a synchronizing program based on earlier sculpture. The ribs appear to be collabral, and therefore their varying orientation reflects a change in inclination of the outer lip during growth.

There are particularly good examples of synchronized sculptures in the genus *Pyrazus* Montfort, 1810 (Fig. 10A-D). The Paleogene *Pyrazus pentagonatus* (Schlotheim, 1820) as the name suggests, has a prominent base-5 pattern of ribs (Fig. 10A-B). Other species of *Pyrazus* display a similar base-7 pattern (Fig. 10C-D). The last whorl may be characterized by a countdown process that changes the character of the sculpture and terminates with a flared outer lip (Fig. 10E). In the illustrated specimen, the synchronization became disrupted due to repaired damage to the aperture (approximately two whorls before the aperture), was gradually regained over the span of one whorl, then lost again as the adult stage approached. Common to all these species with a synchronized pattern is the fact that the sculptural elements consist of collabral ribs extending across the whole outer lip, rather than spiral rows of isolated tubercles. In the latter type of sculpture, spiral rows of tubercles of different sizes often display

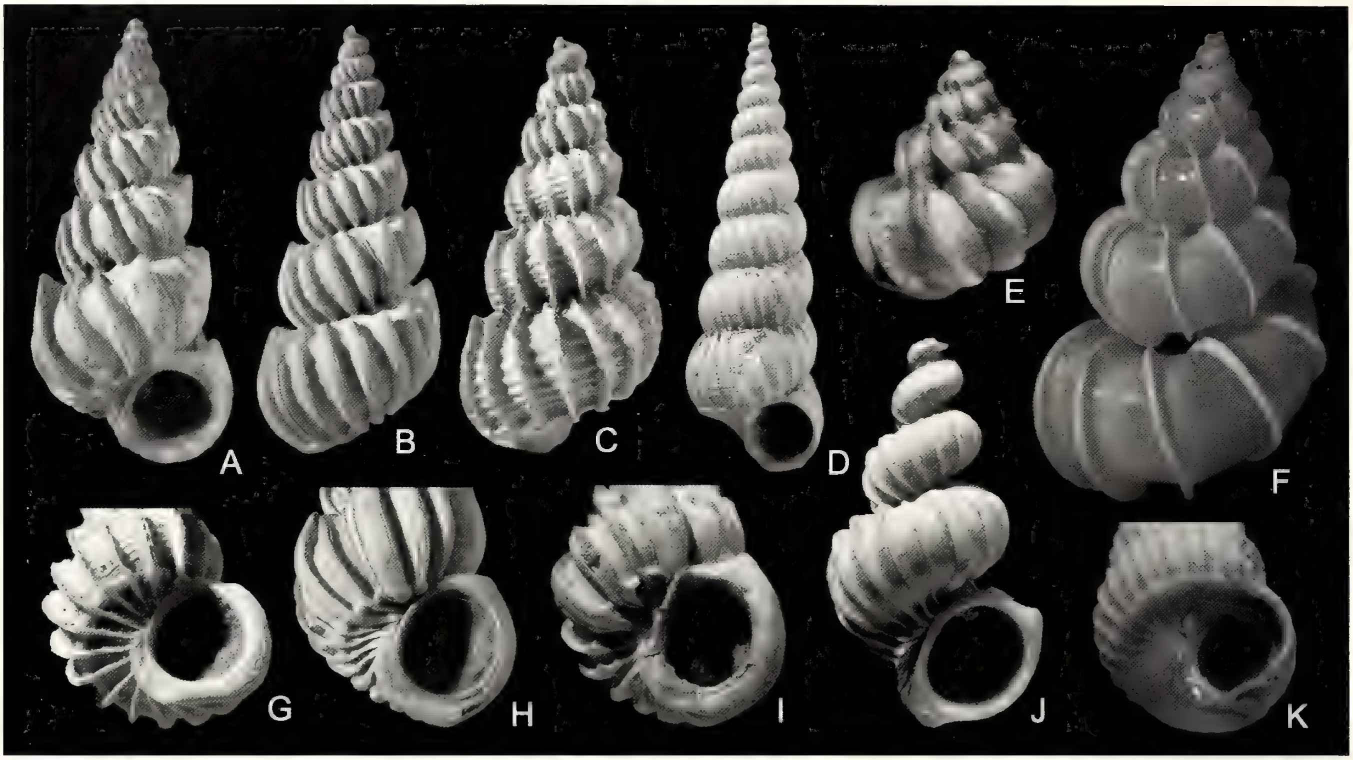

Figure 11. Epitoniidae. A-B, H-I. *Epitonium acutum* (Sowerby, 1813), Eocene, Barton Beds, Barton, UK, 23 mm (A-B, H), 19 mm (I) (CU, A-B, H: C57480, I: C57477). C, G. *Epitonium* sp., Eocene, Barton Beds, Barton, UK, 18 mm (CU, C57470). D, K. *Acrilla reticulata* (Solander, 1766), Barton Beds, Barton, UK, 19 mm (D) and 16 mm (K) (CU, D: C57518, K: C57520). E. *Stenorytis retusum* (Brocchi, 1814), Pliocene, Castell'Arquato, Italy, 17.8 mm (NHM). F. *Epitonium scalare* (Linnaeus, 1758), Recent, Cebu, Philippines, 40 mm (ES). J. *Epitonium spiratum* (Galeotti, 1836), Lower Barton Beds, Highcliff, Barton, UK, 25 mm (CU, C57477).

a different pitch (*i.e.*, periodic angular intervals) of tubercles. The species in Fig. 10I, which is traditionally regarded as a cerithiid but might instead be a turrid, is discussed below.

Bunji Tojo (pers. comm.) and Tojo and Masuda (1999) reported synchronization of the sculpture in the Neogene potamidid *Vicarya yokoyamai* Takeyama, 1933. The sculpture in this species consists of a spiral row of major blunt spines along the posterior region of the periphery of the whorl, sometimes accompanied by other rows of lesser tubercles. He reported synchronization throughout most of the shell, albeit with a break in synchronization (corresponding to a sudden change in the number of tubercles per whorl) roughly midway through growth. His explanation for this synchronization is discussed in the following section. Several instances of similar, apparent synchronization with one or more sudden breaks can be found in a few morphologically similar forms from the Tethyan Paleogene. As a whole, this sculpture is similar to that displayed by several Paleogene species of *Pyrazus* and *Tympanotonos* Schumacher, 1817. The question of whether these instances are a true synchronization is discussed in the next section. Recent species of the potamidid genera *Tympanotonos* (Fig. 10F-G) and *Pyrazus* possess a similar sculpture, but lack synchronization.

Epitoniidae

These are free living, but normally associated with cnidarians, on which at least some species feed. They are found in the intertidal to abyssal zones.

This family is characterized by regularly spaced varices, reinforcing an otherwise thin shell (Fig. 11, Clench and Turner 1951, Bouchet and Warén 1986). Shell growth, including the construction of the varices, can be extremely rapid in this family (Robertson 1983). The thin portion of the shell between successive varices is built in a single episode, which explains the extreme scarcity of specimens observed without a terminal varix. Although varices in studied species were built at relatively regular intervals, these intervals were observed not to coincide with a daily cycle (Robertson 1983).

Clench and Turner (1951) reported that *Epitonium* sp. grows by covering the surface of the preceding whorl with shell material, without removing the earlier sculpture. Our observations confirm this mechanism to be general in the Epitoniidae.

Synchronization of the varices is evident in many (albeit not all) epitoniids, in which varices form uninterrupted series arranged in an antero-posterior or slightly spiraling fashion (Fig. 11A-B, D-F). A large number of species, like

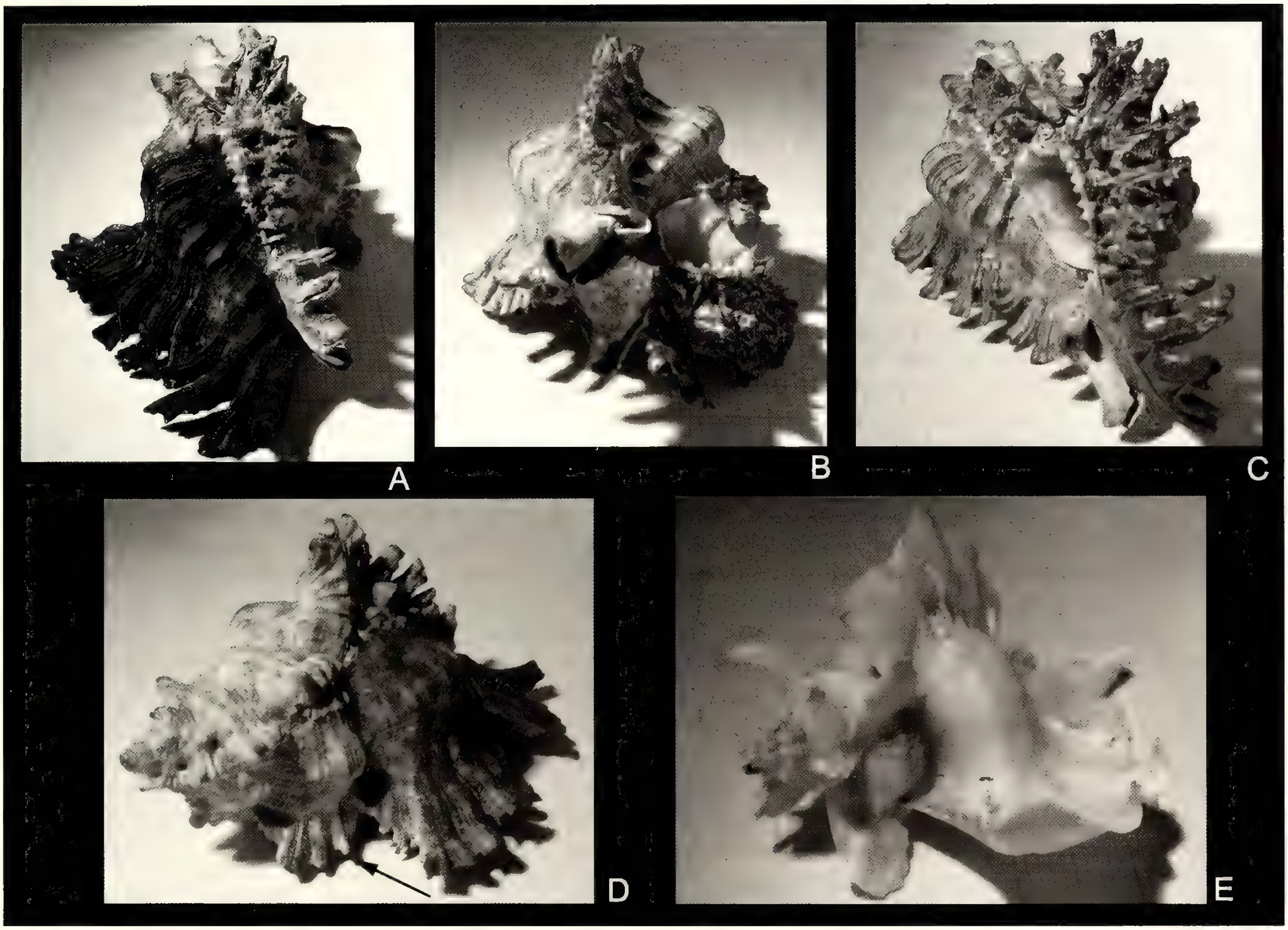

Figure 12. Effect of varices on stable positions of the shell. A-D. *Chicoreus brunneus*, Recent, Cebu, Philippines, 62 mm (ES) (the arrow in D indicates the point where the varix located one whorl back from the aperture touches the substrate). E. *Pteropurpura adunca*, Ushibuka Fishery Port, Amakusa Islands, Japan, 49 mm (ES). All photographed on millimeter paper.

Epitonium scalare (Linnaeus, 1758) (Fig. 11F), possess successive whorls that touch each other only in correspondence of the varices. In several epitoniids, synchronization of the sculpture is occasionally lost in proximity of the adult stage (*e.g.*, last whorl in Fig. 11F; note that the last few varices are not in contact with those of the preceding whorl). In other taxa, synchronization takes place only in the juvenile stages (*e.g.*, Fig. 11C).

In general, epitoniids with few strongly developed varices tend to show a better synchronization than those with many weak varices, although a few species with strong varices lack synchronization on the adult whorls. In species that alternate the construction of thin varices with occasional thicker ones, the latter may disrupt synchronization, which subsequently is regained after a few thin varices. This may be due to a thickened varix requiring a substantially longer period of shell secretion (the amount of shell material in a thickened varix can be estimated to be several times that in a thin one), thus disrupting the normal rhythm of shell growth.

Many epitoniids possess a strong spiral cord around the base of the whorl, or a corresponding nodosity of the varices in the same region. In all the species we observed, the suture of the following whorl is consistently placed in correspondence of this spiral feature (*e.g.*, Fig. 11A, C-D, G-K). This is true of species belonging to different genera and displaying very different amounts of whorl overlap.

Turridae

This family was not investigated in detail. However, synchronization seems to take place in isolated species of Mangeliinae, such as *Mangelia* spp., *Drillia* spp. and especially *Ithycythara* spp. (Warmke and Abbott 1961, Jung 1969). In particular, the Recent *Ithycythara parkeri* (Abbott, 1958) and the Neogene *I. hilaris* Jung, 1969 possess a remarkable base-5 and base-7 pattern, respectively, of rounded ribs. The Eocene species in Fig. 10I (traditionally regarded as a cerithiid) may belong to this or a related genus, and possesses a very regular base-5 pattern. Aside from these instances, Turridae in general display no synchronization, or only questionable examples (Bouchet and Warén 1994, Powell 1966).

Ellobiidae

These pulmonates are broadly adapted to the supralittoral zone of seashores, estuaries and mangrove swamps in tropical to subtropical areas, and graze on the surface of the substrate.

Most of these gastropods display determinate growth, with a single adult varix marking the end of shell growth. *Ellobium* spp. sometimes also displays one or more additional varices placed at variable positions on the last whorl. The genus *Pythia* Röding, 1798 (Fig. 9A-C), instead, possesses a regular base-2 pattern of varices, which can be traced for most of the whorls. The surface of the whorl between varices is flattened, so that the shell has a markedly oval, rather than circular cross-section. This effect is especially marked in large individuals. In a few species of *Pythia*, this is further enhanced by the presence of a broad umbilicus-like depression (produced by partial uncoiling of the anterior portion of the last whorl), also flattened in the dorso-ventral direction, in the adult stage. The internal projection of the varices and all apertural teeth associated with varices are secondarily resorbed from the internal shell surface, and only the internal characters associated with the apertural varix remain.

An undetermined Recent species of *Cassidula* Férussac, 1821 from Cebu, the Philippines, is similar to *Pythia* spp. in general shell proportions (albeit it has no dorso-ventral flattening), but possesses from 0 to 6 varices, in addition to the apertural one, placed at angular intervals that vary (roughly 360-450°) among individuals, and sometimes within the same individual. Some individuals show up to 3 juxtaposed or slightly out of phase varices. Since *Cassidula* spp. typically builds only one apertural varix at the end of the growth process, this form could represent an incipient convergence with *Pythia* spp.

Turbinidae

While most representatives are grazers on hard substrates, *Guilfordia* spp. lives on sandy bottoms at lower subtidal to bathyal depths. The peripheral spines of some species are extremely long. As noted by Linsley *et al.* (1978), these spines project radially, and therefore cannot support the shell above the substrate as do the equally long but downward-bent spines in other families. The substrate preferences of *Guildfordia* Gray, 1850 are also reflected in its non-clamping aperture. On muddy bottoms, the spines probably stabilize the shell on the substrate and increase the effective surface of the shell without substantially increasing its weight, therefore acting like snowshoes.

Guilfordia spp. is characterized by peripheral spines of lengths that vary among species. Spines on earlier whorls are removed by the mollusc, rather than being enveloped in the new whorl. For species with very long spines, like *Guilfordia yoka* Jousseaume, 1888 (Fig. 9I) and *G. triumphans* (Philippi, 1841), this is obviously a necessity. In these species, the bases of early spines remain visible along the suture line (arrows in Fig. 9I). The arrangement of these spines is usually juxtaposed on at least the last few whorls (except for the last 2-3 spines, which in adult specimens may be closely spaced, as in the figure). In species with short spines (Fig. 9J), the bases of the spines are completely covered by the following whorl. In *Guilfordia aculeata* Kosuge, 1979, abrading the shell reveals the same juxtaposition observed in *G. yoka*. This regularity suggests that synchronization is a general phenomenon in the genus *Guilfordia*.

Other turbinid genera (*e.g.*, *Astralium* Link, 1807 and *Bolma* Risso, 1826) possess peripheral spines that typically remain exposed above the suture, rather than being resorbed. The species we observed do not display a consistent juxtaposition.

In many turbinids, the whorl suture follows a spiral rib located on the surface of the preceding whorl for most or all of the growth process. Sometimes, this spiral rib is stronger than surrounding ones (*e.g.*, *Turbo argyrostomus* Linnaeus, 1758; *T. coronatus* Gmelin, 1791; *Astralium henicus* [Watson, 1879]).

Strombidae

These are shallow-water gastropods, mainly tropical and subtropical, normally found on soft bottoms, and characterized by a jumping mode of locomotion (Savazzi 1991).

Representatives of the genera *Rimella* Agassiz, 1840, *Ectinochilus* Cossman, 1887 (including several related genera and/or subgenera) and *Varicospira* Eames, 1952 possess collabral ribs on most or all of the shell. In Paleogene species of *Rimella* and *Ectinochilus*, ribs are not aligned consistently into synchronized series. Among the exceptions is a strongly sculptured morph of *Ectinochilus canalis* (Lamarck, 1804) from the Middle Eocene of NE Italy (Fig. 9R), which shows the regularity of alignment to be expected in true synchronization. In the normal morph of this species, the sculpture decreases in strength on the last whorl and the spacing is usually reduced. Judging from the limited material available and from illustrations in the literature (*e.g.*, Clark and Palmer 1923), the American Paleogene *Ectinochilus macilentus* (White, 1889) and *Cowlitzia canalifera* (Gabb, 1864) may possess a similar synchronization, at least in the pre-adult stage.

In the genus *Rimella*, the ribs frequently appear to be synchronized in the early and intermediate whorls, which are devoid of thickened varices. However, the onset of the first varix almost invariably disrupts the alignment of subsequent ribs with those on the preceding whorl (Fig. 9G). There are morphs of Eocene *Rimella fissurella* (Lamarck, 1803) in which the strength and spacing of collabral ribs increase markedly in the last 1-2 whorls, thus destroying any possibility of synchronization in the adult stage.

In the Paleocene *Mauryna plicata* (d'Archiac and Haime, 1854) collabral ribs are particularly strong and evenly spaced. They appear to be synchronized very consistently, except on the last half-whorl preceding the adult outer lip (see Jung 1974: pl. 16). In this region, however, coarse ribs alternate with much shallower ones, and almost all ribs, regardless of size, join the corresponding ribs of the preceding whorl across the suture. The reliability of observations on *M. plicata* is hampered by the fact that few specimens of this species have been illustrated adequately. Nonetheless, the Eocene *Mauryna bellardi* (de Gregorio, 1880) shows a comparable synchronization of the sculpture in the juvenile portion of the shell (Savazzi 1988). The adult portion of the shell in this species is smooth. Synchronization is also likely in the Paleogene genus *Strombolaria*.

Turbinellidae

Several species in the genus *Vasum* display an apparent synchronization of the varices. This is especially common in species that possess 6 to 9 rows of varices per whorl (Vokes 1966). Species with a substantially higher number of varices per whorl normally display no consistent alignment of the sculpture across successive whorls.

Volutidae

In most volutids there is no clear synchronization of the sculpture (*e.g.*, see Poppe and Goto 1992). However, in isolated cases the sculpture on subsequent whorls is aligned with sufficient regularity to suggest the existence of a synchronizing process. One such example is the genus *Falsilyria* Pilsbry and Olsson, 1964 (see Pilsbry and Olsson 1954). The morphologically similar genus *Lyria*, however, displays no synchronization, since the amount of angular offset between varices on successive whorls often is highly variable within the same individual.

Other families

Several instances of juxtaposed sculpture on adjacent whorls were found in other families, *e.g.* Nassariidae, Mitridae, Costellariidae, Fasciolariidae and Melongenidae. For instance, several fasciolariids in the genera *Fusinus* Rafinesque, 1815, *Latirus* Montfort, 1810, and *Dolicholatirus* Bellardi, 1884 possess apparently juxtaposed sculptures (*e.g.*, see fasciolariids in Abbott and Dance 1983). However, we did not find among these any unquestionable examples of synchronization. In most instances, the pattern of juxtaposition does not remain constant for more than a few whorls. In other instances, many individuals were found to possess non-juxtaposed sculpture.

Fig. 9Q shows an apparent synchronization, but displays a break in juxtaposition between the fifth and sixth whorl, corresponding to repaired damage to the aperture. The pattern regains juxtaposition only after one complete whorl, and the subsequent pattern remains offset from the one preceding the breakage, thus suggesting that pattern formation is not controlled by a synchronizing feedback based on sculpture on earlier whorls, but only by the beating of an endogenous clock. Figs. 9D and 9H are examples of juxtaposition being lost in the last whorl.

Figs. 9E-F show a rather constant juxtaposition (except near the aperture), but with small disruptions that appear to be "repaired" quickly. This would suggest a synchronizing program, but, especially in forms with a large number of sculptural elements per whorl, there is a certain amount of subjectivity in deciding when sculptural elements are juxtaposed but slightly offset with respect to each other, and when the amount of offset is sufficient to declare them to be non-juxtaposed. This example is typical of one of the main problems encountered in our survey. In other instances, the pitch, or angular interval, of periodic sculptures changes gradually and very visibly during ontogeny, producing non-synchronized patterns easy to detect (Fig. 9G). In a few instances, isolated species within a genus seem to possess a synchronized sculpture, while all other representatives display a poor or absent juxtaposition. One such example is *Harpa articularis* Lamarck, 1822, which seems to display a consistent juxtaposition of varices between the last and penultimate whorls, while all the other Recent species of *Harpa* Röding, 1798 we were able to observe show evident breaks in juxtaposition.

DISCUSSION

While it is true that apertural varices with their associated characters, as well as other types of sculpture, have been shown to possess a broad variety of functions, and that several of these functions rely on the periodicity of sculpture (Vermeij 1971, 1979, 1981, 1982, 1983, Palmer 1977, 1979, 1980, Spight and Lyons 1974, Bertness and Cunningham 1981, Donovan *et al.* 1999), the following discussion concentrates on themes related to synchronization, and does not deal with the function of non-synchronized sculpture, or with functions that can be carried out equally well by synchronized and non-synchronized sculpture. Likewise, the discussion of morphogenesis deals with synchronizing mechanisms, not with the construction of individual sculptural elements.

Function of base-1 patterns

This type of pattern is found only in the Eulimidae. Curved eulimids with base-1 patterns are typically ectoparasites on echinoderms (Warén 1983, Bouchet and Warén 1986). Their attachment to the host is not permanent. The curved shell geometry may be adaptive in this context, since the concave side of the shell is located roughly on its right side. When the gastropod contracts the columellar muscle while attached to the host, the outer lip of the aperture is drawn against the surface of the host, and the shell lies with the apex curving toward the substrate, *i.e.*, flatter against the host than would be possible for a straight shell. This may make the shell less likely to be dislodged by predators or accidental impacts.

The growth lines and apertures of many curved eulimids are opisthocline. Thus, the anterior region of the outer lip touches the substrate first, and causes the shell apex to be pushed close to the substrate when the shell clamps against it. A prosocline aperture would provide a better seal of the aperture against the substrate, but would cause the apex to point away from the substrate. Thus, opisthocline growth lines may be coadaptive with shell curvature in minimizing the projection of a clamped shell above the surface of the substrate. The extreme smoothness of the shell also may be coadaptive in this respect.

These adaptations, however, would be most effective on a flat substrate, while echinoderm hosts often display a prominent relief. In addition, several ectoparasitic eulimids are straight-shelled, while a few representatives with curved shells possess strong sculpture. These forms do not support the above hypothesis.

Another possible interpretation is based on the fact that the curvature of the columella is associated with a slight outward flaring of the outer lip, which in turn allows the construction of a thickened outer shell lip without restricting the internal lumen of the shell in this region. Aligning all thickened and flaring regions on the same side of the shell prevents them from projecting from the shell at different positions, and thus from providing an uneven surface that may help a predator to hold the shell steadily. However, it must be admitted that the evidence in favor of or against the above functional hypotheses is insufficient to allow a decision.

Morphogenesis of base-1 patterns

The curved shell geometry in the Eulimidae is always associated with a base-1 pattern. Eulimids that lack synchronization or possess base-2 patterns have straight shells. In addition, in cases in which the incremental scars in a base-1 pattern display an angular offset between successive whorls, thus causing the pattern to spiral markedly around the shell, the shell curvature spirals in the same way. In these cases, the shell can be more correctly described as slowly corkscrewing, rather than curving (*e.g.*, Fig. 1A-D). Thus, there is a clear causal connection between the base-1 sculpture pattern and shell curvature in the Eulimidae. A very similar situation occurs in the buccinid *Colubraria tortuosa*.

It is easy to see that an evenly curved (or corkscrewing) shell can be achieved only by a base-1 pattern: curved shell increments in a base-2 or higher pattern cancel out each others' curvature. This is seen, for instance, in the genus *Distorsio*. In this genus, each growth increment between varices deviates conspicuously from a regular spiral, and the columella is visibly bent, but, on a larger scale, the bends cancel each other out.

In other families, shells with curved columellas occasionally result from accidents (usually damage to the shell and, possibly, to the mantle; Fig. 1J-L). However, in most of these cases the result is a sudden curvature of the shell from one whorl to the next, not repeated on subsequent whorls (Fig. 1J-K). More rarely, the curvature seems to be synchronized across two or more whorls (Fig. 1L). The latter instances, however, generally occur in taxa in which the shells display a large amount of whorl overlap, so that the effects of a sudden deformation of a single whorl affect several subsequent whorls.

Some of the straight-shelled eulimids possess irregularly distributed incremental scars, corresponding to internal thickenings (albeit not as marked as in curved taxa) and pauses in shell growth. In some of these forms, the incremental scars trigger the formation of a slight depression near the suture of the subsequent whorl (Fig. 1G-I). This suggests that the basis of the morphogenetic process responsible for triggering the synchronization of the internal incremental scars is present, albeit not entirely operational, in these forms.

That feedback from the immediately preceding whorl is important in the synchronization of sculpture in the eulimids is suggested by the fact that repaired damage to the shell aperture (arrow in Fig. 1M) sometimes causes an offset in the placement of the subsequent incremental scar, while all other preceding and following incremental scars are placed properly with respect to each other. Thus, this disturbance results in two sets of incremental scars misaligned with respect to each other (Fig. 1M). This indicates that the constructional process that synchronizes the sculpture may receive a feedback signal exclusively from the immediately preceding whorl, with earlier whorls playing no part in the program. This is consistent with a feedback generated by tactile sensing of relief on the external shell surface of the penultimate whorl. This surface is readily accessible to the mantle because the next whorl is attached to it, but it is unlikely that the mantle can extend to touch the outer surface of whorls preceding the penultimate.

It is probable that these elements of the synchronization mechanism are part of a family-wide Bauplan (usually defined as the set of shared morphological characters and constructional/morphogenetic mechanisms, not necessarily expressed in all representatives of a supraspecific taxon, but supposedly shared by all or most representatives). In fact, the curved morphology likely evolved multiple times within the family (A. Warén pers. comm., 1983), so the existence of a common set of constructional elements shared also by non-curved representatives of the family (and sometimes expressed as non-functional, incipient incremental scars triggered by scars on the preceding whorl) is probable. Also, a very similar process may be involved in the construction of base-1 and base-2 patterns in this family.

A general morphogenetic hypothesis

Based on the above observations, we hypothesize a general growth process in which the fabrication of the first incremental scar, or apertural varix, is triggered endogenously. Afterwards, the signal for the construction of further varices is provided by tactile feedback from corresponding morphological features on the preceding whorl(s). This feedback can be generated by the soft parts touching earlier portions of the shell, either on external or internal shell surfaces. In the case of feedback from external features, the mantle tissues must extend outside the aperture, and its reach may be limited to a relatively small portion of the shell (typically including the ventral region of the penultimate whorl). This is consistent, for instance, with observations on the Eulimidae (see above). In the case of feedback from internal shell features, in principle the whole extent of the soft parts within the shell can have a sensing function, and therefore the entire shell cavity may be available for morphogenetic cues. This difference suggests a way of ascertaining which source of feedback is being used by a particular taxon: in the presence of accidental disturbances, the two alternative programs should react in different ways.

In addition, in the occasional absence of a feedback signal, construction of a new varix may be triggered once a maximum time has elapsed from the construction of the last varix, or a maximum extent of shell surface has been built after the last varix. Such a mechanism would constitute an effective "insurance" against accidental disruptions of the pattern. In the absence of such a mechanism, we should observe the construction of new varices to take place only as a result of feedback from earlier sculpture. For instance, in the case of curved eulimids, the accidental absence of an incremental scar would result in the rest of the shell being devoid of such structures. Also in this case, comparison of this predicted behavior with actual shells will enable us to decide whether such a process takes place in gastropods.

Finally, a mechanism ensuring that a minimum time must elapse (or a minimum extent of shell whorl must be secreted) before a new varix can be built may help in rejecting spurious feedback signals. This property, as well as the preceding one, are common in regulatory systems (Meinhardt 1995).

The observations carried out on other gastropod families and described in the preceding sections can be used to test these ideas.

Muricid sculptures

In this family, base-3 and base-5 patterns are especially common, while base-2 and base-4 patterns are rare (Ponder and Vokes 1988, Houart 1992). A strong functional reason for this is that patterns with odd-numbered bases result in a varix (and associated spines and/or wing) projecting in the dorsal direction. This is not true of even-based patterns. As shown in Fig. 12B-C, a dorsal varix prevents an overturned shell from lying on the substrate with the aperture facing directly upwards, and forces the aperture to be inclined toward either side. In turn, this is likely to make it easier for the gastropod to right its shell.

This effect is especially pronounced in base-3 and base-5 patterns. Shells with these patterns tend to settle with two adjacent varices resting on the substrate on either side of the shell, thus functioning like stabilizing "outriggers" (Fig. 12A-C). Base-7 and base-9 patterns, instead, are not substantially different from base-6 and base-8 patterns, because the varices are so closely spaced that the outline of the whorl approximates a circle. Thus, base-6 and higher base patterns all behave in a similar way. None of these patterns prevents a shell from lying with the aperture pointing upwards, but, at the same time, their sculpture is not a serious obstacle to righting, especially if the varices and associated sculpture are only moderately developed. We believe this is why base-6 patterns are moderately common in muricids, and base-3 patterns usually possess the broadest wings, with base-5 patterns bearing somewhat more subdued projections (albeit, exceptions do occur).

That a dorsal righting projection is of paramount adaptive importance is shown, for instance, by the morphology of the adult whorl in strombid gastropods. This family displays a determinate growth pattern and an adult aperture typically flaring into a broad wing and/or carrying large spines and projections. Most strombids also possess a dorsal knob or projection. As discussed by Savazzi (1991), these features in strombids facilitate righting by inclining the overturned shell to either side. The same adaptive significance can be attributed to the dorsal varix in muricids with base-3 patterns and, perhaps to a lesser extent, in base-5 patterns. In base-3 patterns, the two ventral varices, being located on either side of the aperture, can stabilize the shell in the life position. However, they also make righting more difficult, as does the flaring aperture of adult strombids. The problem is alleviated, of course, by the presence of a dorsal varix. In base-5 patterns, an overturned shell can land in any of four stable positions, of which two are close to the life position (the aperture being inclined only 70° from the horizontal), and do not impede righting in a substantial way. The remaining two positions (*i.e.*, with the dorsal varix in contact with the substrate, and the aperture pointing obliquely upwards) pose a more serious problem.

A similar situation occurs in gastropods with other periodic growth patterns. For instance, adult *Cassis cornuta* possess a large dorsal tubercle, which is absent on earlier growth increments (Savazzi 1994). In the present study, dorsal tubercles were observed in bursids (Fig. 6E, I). The same function can be attributed to the other instances of dorsal tubercles discussed above. In species that keep the coiling axis of the shell inclined, rather than horizontal (*e.g.*, Fig. 6E, I), righting tubercles can also be built on subadult growth increments, but typically reach their full development only in adults.

In species that hold the shell with the coiling axis substantially inclined, an angular offset between the juxtaposed varices on successive whorls is not especially detrimental, since the spire is rather distant from the substrate. In some cases, such an offset might be desirable, since it places the varix on the penultimate whorl closest to the shell aperture in a position that partly protects access to the aperture, and may also function to stabilize the shell by adding a point of contact with the substrate posterior to the aperture (arrow in Fig. 12D).

Muricids with this type of angular offset between varices on successive whorls hold their prey steady by wedging it in the space between the apertural varix and the corresponding varix on the penultimate whorl, or use the latter varix to pry open bivalve shells (Illert 1981, other muricids use seemingly better methods, like specialized apertural spines; *e.g.*, Paine 1966, Vermeij 1983, Malusa 1985, Perry 1985). In this case, the offset may be functional, and this may explain occasionally large offsets (Fig. 12E), which actually prevent effective clamping against the substrate.

The adaptive advantage of base-5 patterns may be a compromise between stabilization and other functions. For instance, base-5 patterns allow a significantly closer spacing of the varices than do base-3 patterns, thus allowing an alternation of more numerous but presumably shorter periods of growth and stasis. Closer-spaced varices may also provide better protection from shell-peeling predators, put at risk from these predators a shorter region of the shell, and require the soft parts to be retracted a shorter distance within the aperture in order to be protected by the preceding, fully thickened varix.

There appears to be a general qualitative trend in muricids (admittedly, with numerous exceptions) of base-5 and higher patterns being associated with short spired and/or small shells, while base-3 patterns tend to be concentrated among relatively large and high-spired forms or forms with a long anterior siphon. The latter group includes principally *Murex s.s.* and *Haustellum* Schumacher, 1817 (see Ponder and Vokes 1988). *Bolinus* is an exception, as it has a long siphon but several (typically 7 to 9) varices per whorl, often with breaks in the synchronization pattern.

The existence of this trend needs to be verified quantitatively. Nonetheless, muricids with short, paucispiral shells can likely retract a shorter distance within the shell than can species with high spired, multispiral shells, and therefore it could be advantageous for the former to have a larger number of varices per whorl.

In *Murex pecten* and other species with long and numerous siphonal spines, the original stabilizing function of the base-3 pattern may be supplemented by a protective function (Paul 1981). A similar function may also be hypothesized for muricids with extremely broad wings. Even more modest varices, wings, and sets of spines with a primary stabilizing function do offer a measure of protection of the soft parts, and this provides a plausible stepping-stone to the evolution of highly specialized protective sculptures like those of *M. pecten*.

Individuals of the genera *Aspella* Mörch, 1877 (Fig. 4A-C, G), *Eupleura* H. and A. Adams, 1853 (Fig. 4D, H), and *Phyllocoma* Tapparone-Canefri, 1881 possess well-developed base-2 patterns. The main varices in species of *Aspella* alternate with two swellings or minor varices. The first swelling that follows the preceding varix is very weak, and developed only near the suture. The second swelling is stronger, and functions as a small outrigger along the left side of the shell (see Fig. 4G).

Eupleura caudata possesses two tubercles between successive varices (Fig. 4H). These tubercles are equally developed and form outriggers, albeit rather close to each other. The two varices projecting from either side of the shell probably prevent overturning in case the tubercles do not suffice.

Species of the genus *Phyllocoma* do not display a subdued axial sculptures intercalated with the varices. The large amount of angular offset (up to 60°) between varices on successive whorls results in the last and penultimate varix forming outriggers on either side of the aperture, and therefore the sculpture is likely optimized as a stabilizer.

In these three genera, different solutions appear to have evolved to the same problem: namely, that a pattern consisting of only varices spaced 180° from each other would not allow both varices to touch the substrate simultaneously (because of the intervening bulk of the shell whorl). Each of the modifications to this pattern discussed above may therefore enhance the stability of the shell on the substrate, and most likely represents an instance of parallel evolution.

The Recent typhine *Distichotyphis vemae* Keen and Campbell, 1964 is the only representative of this subfamily with a base-2 pattern. The posterior tube located closest to the aperture points obliquely in the dorsal direction, as in species of the Typhinae with larger numbers of varices per whorl. Therefore, the adaptive significance of the posterior tubes in *D. vemae* does not seem to be a stabilization of the shell (*cf.* section on base-2 patterns, below).

Synchronized patterns in Cerithioidea

The shells in representatives of this superfamily studied herein are more elongated than in the Muricidae, and are usually dragged on the substrate, rather than being balanced on the soft parts, as in muricids. However, synchronized sculpture less developed than that of the Muricidae still can be functional in increasing shell stability on the substrate, since the sculpture is constantly in contact with the substrate. It seems likely that the odd-based synchronized patterns in the Cerithioidea are convergent with the Muricidae and that the sculpture facilitates shell righting in both families. In fact, the best examples of synchronized sculpture in this superfamily are found in the Potamididae, and are base-5 and base-7 (Fig. 10A-D). The last few whorls possess a significantly larger surface than do earlier ones, and therefore, even a sculpture pattern that spirals around the shell (instead of being arranged in an antero-posterior direction) is likely to be functional in this context. A simultaneous function of these sculptures as buttresses (see below) is also likely.

Function of synchronized sculpture in the Coralliophilidae

The adaptive significance of synchronization in *Babelomurex* is uncertain, since the spines in this genus normally do not touch the substrate in a way that suggests an optimization to a stabilizing function. Although the spines do increase somewhat the effective area of contact with the substrate, they also project high above it, thus increasing the chances of dislodgement by external agents. In addition, the potentially vulnerable area above the head of the gastropod is not protected by these spines. Unfortunately, the life habits and position relative to the substrate of these spiny representatives is unknown.

Long spines in this genus are more likely a protection against predators (both shell crushers and predators that would swallow the prey whole), and are functional in increasing the overall size of the shell (by up to 400% in effective diameter), thus making it difficult or impossible to handle. However, synchronization does not appear to offer a particular advantage in this context (and in fact, other coralliophilids display no synchronization; see also below).

Base-2 patterns without dorsal projections

Many gastropods with base-2 patterns do not build dorsal projections. This is the case in some bursids (Fig. 6A-C, F-H; see also below), as well as all eulimids, cassids, ranellids and ellobiids with base-2 patterns observed in this study (see above for a discussion of base-2 patterns in muricids). In these cases, a premium is apparently placed on building a shell that projects only minimally above the substrate, as shown by the frequent instances of subdued sculpture on the dorso-ventral surfaces, and/or dorso-ventrally flattened whorls. This idea is also supported by the fact that this sculptural pattern is generally associated with a coiling axis subparallel to, or only moderately inclined with respect to, the substrate.

The occasional base-2 patterns found in the Eulimidae, unlike base-1 patterns in the same family, usually are associated with prominent varices and associated projections (*e.g.*, Fig. 1N-O). Their general effect is of increasing the cross-section of the shell laterally (up to 300% in *Hoplopteron* Fischer, 1876 (= *Ptereulima* Casey, 1902), Warén 1983). Too little is known about these forms to hypothesize about their function.

In most or all instances of base-2 patterns lacking dorsal projections, this character provides a broad resting surface onto the substrate, and a correspondingly low profile above the substrate. This would enhance the clamping action of the foot onto a solid substrate, a particularly important adaptation for hard-bottom dwellers. A base-2 pattern may also be advantageous in soft-bottom forms, in which it is likely to stabilize the shell in an epifaunal or semi-infaunal life position. Apparently, in all these forms the primary adaptive significance of shell geometry is minimizing the risk of detachment from the substrate and/or overturning in the first place, while in the forms with dorsal knobs the emphasis may be on facilitating righting *after* overturning takes place. In *Biplex* spp., the presence of morphs with a median region of the whorl depressed and devoid of sculpture (Fig. 7H) may represent a convergence with the muricid genera *Aspella* and *Eupleura*.

In the ellobiid genus *Pythia* (Fig. 9A-C), the last varix and associated dentition provide a defense against predators. Earlier varices have the same function when located at the aperture, but subsequently lose this function, since the dentition is secondarily resorbed. The base-2 pattern may have evolved from a non-synchronized ontogenetic sequence of varices, which provides better protection during growth than a final pattern does indeed occur in at least one ellobiid (see above). The adaptive significance of synchronization and of the period of 2 likely lies in the dorso-ventral flattening of the shell that they permit. As noted by Paul (1999), the shells of land snails limit access to sheltered locations, like crevices. As a consequence, the size of shell-bearing land snails found in restricted quarters (*e.g.*, under the bark of fallen trees, or under stones) is much smaller than the size of shell-less snails (Paul 1999). Dorso-ventral flattening of the shell reduces one dimension of the shell, thus allowing easier movements under flat objects, and does not require a substantial increase in shell length to compensate for the lost volume. *Pythia* spp. is common under dead foliage and wood (pers. obs.), a life habit that supports the above idea. A similar adaptive result can be achieved by flattening the shell along the coiling axis and carrying it with the coiling axis perpendicular to the substrate (as done by many pulmonates), but this also reduces the size of the shell aperture. This adaptive solution may be unavailable to ellobiids, which tend to possess antero-posteriorly elongated shells with rather long apertures.

Base-2 patterns with dorsal projections

These are exceptions rather than the rule, and in this study they have been encountered only in the Bursidae (Fig. 6D-E, I). These projections appear to be righting structures (see above). In forms that keep the coiling axis inclined, instead of parallel to the substrate, dorsal projections may be located above the shoulder of the whorl, and therefore can be repeated in the last few growth increments without impeding locomotion or destabilizing the shell when moved to the ventral shell surface by further shell growth (Fig. 6E).

Base-3/2 patterns

This arrangement of sculptural elements provides two varices on either side of the aperture, and a third varix pointing upwards on the penultimate whorl. Thus, the result is roughly comparable to a base-3 pattern, and differs mainly in the fact that the upward-pointing varix is less prominent (being located on an earlier whorl) than in the latter pattern. As a result, it is less effective in preventing an overturned shell from lying with the aperture pointing straight upwards is less effective. In several species of Ranellidae with base-3/2 patterns, this problem may have been solved by the evolution of projecting dorsal knobs, or a swollen dorsal region on the last whorl, with a similar righting function. This adaptation is absent in the otherwise similar Colubrariinae with base-3/2 patterns.

The dorsal varix in base-3/2 patterns is unlikely to be touched by the mantle tissues on the external shell surface, as it is too far from the aperture. However, as shown in Fig. 7E, in principle this varix can be sensed by the soft parts *within* the shell cavity, and therefore a synchronizing mechanism in this particular case is possible without direct mantle contact with the external shell features.

The shell geometry and its adaptive value in the genus *Distorsio* have been studied by Linsley (1977), Linsley and Javidpour (1980), Stanley (1988), Ackerly (1989), and Checa and Aguado (1992). Some of these authors do not agree in details of their interpretations. Nonetheless, it is evident from Fig. 8A-C that the periodic swellings of the whorl between varices are located near the preceding varix, and that the whorl flattens considerably near the next varix. Therefore, the swelling is not located in an optimal position to function as a righting projection. Instead, the flattening that follows the swelling allows the last apertural varix to form a very good clamping structure against the substrate, and the coiling axis to lie subparallel and very close to the substrate. In other species, this phenomenon is developed to different extents. In species like *D. reticulata* (Fig. 8E-F), this effect is minimal, and the coiling axis forms an angle of 10-15° to the substrate, rather than being parallel to it. Paleogene and Neogene species of *Distorsio* tend to display a moderate amount of swelling and flattening between varices, while there is a broader range of variation among Recent species. The swelling that precedes the flattened region of the whorl increases locally the volume of the shell cavity, and probably compensates for the volume lost by flattening.

Since the aperture is restricted by a complex dentition, it is unlikely that the flattening is functional in restricting access to the shell interior by predators. In addition, the shell between varices is thin and easily removed by peeling predators, as shown by frequent instances of repaired shell damage inflicted on individuals lacking a fully thickened terminal varix (Fig. 8E). Therefore, whorl flattening in *Distorsio* does not seem to be functional in other contexts than the one described above. If this view is correct, the flattened region is not functional on the last growth increment (*i.e.*, just after being built), but only after a subsequent growth stage is added.

In members of the Cassidae with base-3/2 patterns, the two ventral varices are likely to have a stabilizing function, as described above. The dorsal varix, instead, is unlikely to have any righting function because the diameter of successive whorls in this family increases more rapidly than, for example, in most Ranellidae. In the Cassidae, therefore, the adaptive significance of base-3/2 patterns likely is related only to the two ventral varices. In fact, adult cassids with this pattern not infrequently possess only two varices.

Relationships of base-2 and base-3/2 patterns

In the Cassidae, Bursidae and Ranellidae, both base-2 and base-3/2 patterns occur within groups of morphologically similar and probably related representatives. This suggests that the evolutionary shift between the two types of pattern is relatively easy, and has occurred multiple times, and possibly in both directions. In fact, this can be achieved by a relatively small (about 30°) increase or decrease in the angular distance between successive varices. If we assume that tactile feedback from the preceding varices is involved, base-2 patterns require a feedback from either (1) the corresponding varix on the preceding whorl, *i.e.*, 2 varices behind the one being built, or (2) the penultimate varix, spaced half a whorl away from the current aperture.

In case 1, tactile sensing can be carried out by the mantle in immediate proximity to the aperture. Case 2, instead, requires the mantle to extend to the penultimate varix, half a whorl away. Although the first situation may seem easier and less risky (as it reduces the exposure of the soft parts to potential predators), it involves a morphogenetic drawback. The penultimate varix would not be a part of the feedback process, and therefore an incorrect placement of this varix could not be sensed. As a result, the placement of immediately successive pairs of varices becomes decoupled from each other, and this can lead to gross distortions of the pattern. For instance, in this scenario the two sets of juxtaposed varices could be placed at an angular interval to each other of 120°, instead of 180°, and this error would remain undetected and replicated by each successive whorl. On the other hand, a feedback based on the position of the penultimate varix alone would cause the pattern to regain its regularity after a disturbance (albeit possibly introducing a permanent angular offset with respect to whorls preceding the disturbance).

In members of the Cassidae that have base-2 and base-3/2 patterns (Fig. 9K-N), the penultimate varix is partly covered by a callus located near the anterior region of the aperture (the portion of the penultimate varix closest to the aperture). This callus is proof that the mantle tissues cover this region at least while building this structure, and therefore, that the mantle touches this varix. Therefore, at the very least, this region of the penultimate varix can be part of a tactile feedback system. Other varices seem to be too far from the aperture to be reached by the mantle (at least on the external shell surface).

Indirect evidence for tactile feedback in sculpture synchronization

A spiral cord, or a spiral series of knobs on successive varices (Fig. 11G-K), is common on the anterior region of the whorl in the Epitoniidae, and marks the position of the suture of the following whorl. It is likely that this spiral feature is used as a morphogenetic cue for placing the following whorl in a correct position. A similar situation, likely with the same significance, occurs in some turbinids in which the suture corresponds to a particularly strong spiral cord on the penultimate whorl. The sharp peripheral keel of the trochid genus *Calliostoma* Swainson, 1840 and similar forms may have the same function. It seems very likely that the feedback signal involved in sensing the position of this cue is tactile and generated by the mantle tissues touching the preceding whorl.

As discussed by Hutchinson (1989), in many gastropods the shape of the preceding whorl is used as a cue for placing the current one correctly via a "road-holding" mechanism. The use of specific sculptures as tactile signals, as described above, makes road holding more precise. In addition, this indirectly strengthens the idea of tactile feedback controlling the synchronization of the sculpture, as the two processes are very similar.

In a few species of *Distorsio* part of the apertural callus displays an amplification, or reinforcement, of the sculpture originally present on the surface of the penultimate whorl (Fig. 8G-K). Clearly, this pre-existing sculpture acts as a morphogenetic cue, mediated by tactile sensing by the mantle.

In the Coralliophilidae, synchronized sculpture occurs in representatives of *Babelomurex*, but not in morphologically similar species of *Latiaxis* and other genera. *Babelomurex* differs from the latter in the presence of a second spiral row of smaller spines, or knobs, located below the shoulder of the whorl and juxtaposed to the larger spines placed on or above the shoulder (Fig. 5D, F, H). On the penultimate whorl, the mantle is in direct contact with these smaller spines, which lie below the whorl suture, and therefore can sense their position and use it as a morphogenetic cue. On the other hand, the larger spines located in a more posterior position may not be directly accessible to the mantle. *Latiaxis* and related genera typically lack this additional row of smaller, juxtaposed projections, and therefore synchronization is probably absent in these taxa because no tactile cues are within the reach of the mantle.

In the genus *Guilfordia*, synchronization is associated with selective resorption of the spines projecting from the periphery of the penultimate whorl, which are in contact with the mantle. In the related and morphologically similar genera *Astralium* and *Bolma*, sculpture on the periphery of the penultimate whorl are neither resorbed nor covered by the new whorl, and as a consequence there is no synchronization.

The sum of the evidence strongly suggests that tactile feedback by the mantle tissues is a fundamental part of morphogenetic programs controlling the synchronization of sculptures, the correct placement of the last whorl with respect to the penultimate one, and other phenomena resulting in the generation of morphological features of gastropod shells. At least in the case of synchronized sculpture, the principal, or only, source of tactile information is contact between the mantle and the outer surface of the penultimate whorl. This mechanism is widespread within families, and recurrent in a broad range of distantly related families.

General significance of buttressing

In classical architecture, massive buttresses were used to stiffen large structures like the outer walls and roof-vaults of churches. To be maximally effective, a buttress should be a continuous structure carrying its own weight and the stresses generated by loads on walls and ceilings. In the case of churches with multiple parallel vaults and multiple internal rows of columns, a buttress should brace all vaults as a single structure. This situation is analogous to juxtaposed (and cemented together) varices on successive shell whorls.

A hypothetical building that violates the above principle could possess isolated portions of buttresses placed at different positions and heights along the ceilings and/or walls. In the case of a large building, obviously this would be a recipe for disaster. Non-juxtaposed sculptures on gastropod shells may not be equally critical, since the weight of a shell does not place a significant load on its structure. However, many predators can apply high stresses to the shells of gastropods. In these cases, it can be expected that non-juxtaposed sculptures will channel stresses through thin, as well as thick portions of the shell. This is probably less critical for shells attacked by peeling predators, since these tend to concentrate stresses on a small portion of the shell. In the case of shell-crushing predators, instead, stresses are applied to the whole shell, and juxtaposed sculptures are more likely to distribute these stresses in a way that is advantageous for the gastropod. This may be especially important for gastropods bearing few varices per whorl, in which broad portions of the shell are structurally weak. Likely, buttressing is an additional selective pressure promoting the synchronization, and thereby the juxtaposition, of gastropod shell sculpture. In fact, Donovan *et al.* (1999) reported that individuals of the Recent muricid *Ceratostoma foliatum* (Gmelin, 1791) with varices artificially removed are predated more easily by fish and crabs, and that the latter often snap the shell in half after peeling it. Synchronized varices may make the latter behavior less effective by stiffening the shell as a whole.

In epitoniids with successive whorls that touch each other only in correspondence of the varices, the significance of buttressing as a mechanical reinforcement is obvious, but the shell between varices in this family is so thin that buttressing is likely to be important also in epitoniids with adjacent whorls in continuous contact. The mechanical effects of buttressing by synchronized folds of the shell are likely similar to those of synchronized varices. Therefore, synchronized plication may have a similar reinforcing function in the representatives of the Strombidae, as well as isolated instances in other families, possessing this sculpture pattern.

An alternative mechanism of sculpture synchronization

Bunji Tojo (pers. comm.) reported sculpture synchronization in the potamidid *Vicarya yokoyamai* and proposed a mechanism for this process that does not rely on tactile feedback of earlier sculpture. The spines in *V. yokoyamai* are located high on the shoulder of the whorl, and therefore likely beyond the reach of the mantle. He proposed that the projecting spines cause the shell to lie on the substrate in a stable position, resting on two antero-posterior rows of synchronized spines, and that shell growth eventually causes the shell to topple to the next stable position. He further hypothesized that this sudden change in orientation of the shell is used as a morphogenetic cue to keep the sculpture synchronized. This is an interesting idea that, if verified by further observations, would provide an alternative to tactile feedback, and could explain some of the quasi-synchronized sculptures observed in this study (*e.g.*, in some Turridae and Fasciolariidae). It is not, however, of general applicability. For instance, in the Muricidae the animal changes life habits and goes into hiding during the construction of a growth increment, and therefore the shell orientation with respect to the substrate likely becomes irrelevant as a morphogenetic cue at this time. Tojo's mechanism is more likely to be testable in cases in which a tactile feedback from earlier sculpture (which would seem to be a more reliable mechanism) is not possible.

CONCLUSIONS

Synchronized sculptures on gastropod shells are periodic sculptures built at fixed reciprocal positions across successive whorls. They occur in several gastropod families and have a varied adaptive significance, which includes stabilizing the organism during locomotion, facilitating righting after accidental overturning, enhancing the clamping action against a substrate, and increasing the overall strength of the shell. Regulatory processes are apparently involved in the construction of synchronized sculpture, and in particular in ensuring the proper alignment of sculptural elements across successive whorls. In most instances, observations support the idea that the main factor controlling this synchronization is a tactile feedback provided by the mantle tissues touching the sculpture on the external surfaces of earlier whorls, and in particular the surface of the penultimate whorl in proximity of the shell aperture.

Numerous instances and types of synchronized sculpture emerged from this study. The adaptive significance of synchronization in the Eulimidae, which display the only type of base-1 pattern found in this study (with a possible exception in the Colubrariinae), is uncertain, but there is a clear causal relationship between this pattern and a curved shell.

In the Muricidae, stabilization of the shell (both as a reduction of the risk of accidental overturning and as a facilitation of righting an overturned shell) appears to be the primary function of synchronization. The frequent occurrences of base-3 and base-5 patterns, and the corresponding rarity of base-2 and base-4 patterns in this family are also explained by considerations of shell stability and ease of righting. A similar significance can be ascribed to base-5 and base-7 rib patterns in potamidid cerithioideans. In contrast, the significance of synchronization in the Coralliophilidae, superficially similar to the Muricidae, is uncertain.

In the Bursidae and Ranellidae, various taxa display morphologies that appear especially optimized for one or more of the following functions: prevention of overturning, ease of righting after overturning, and/or effective clamping of the aperture against the substrate. In the Cassidae and Ellobiidae, stabilization during locomotion appears to be the principal function. Mechanical reinforcement by buttressing, instead, appears to be the main function in the Epitoniidae, Strombidae, and a few other instances.

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In celebration of two outstanding molluscan functional morphologists: Drs. Vera Fretter and Ruth D. Turner

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Abstract: The scientific contributions of Dr. Vera Fretter (University of Reading, UK) and Dr. Ruth D. Turner (Harvard University, USA) represent important foundations for the current studies of molluscan functional morphology. The Symposium "New Frontiers in Molluscan Functional Morphology" is dedicated to these two scientists. Although each published on several groups of molluscs, the major contributions and impacts in malacology are, for Dr. Fretter, the prosobranch molluscs, and for Dr. Turner, the bivalve molluscs. Their passion to understand the insides of molluscs, the life histories, and how these functional structures were adapted to particular environments characterized their numerous publications. These studies changed the way people thought about the evolution of molluscs, an area of continuing interest in papers in the symposium presented at the 2001 World Congress of Malacology in Vienna. Drs. Fretter and Turner acted as important role models to young scientists and were well known for their communication and teaching about these molluscs at workshops and post graduate courses around the world. To have been influenced by either one or both of these malacologists as a young scientist was indeed a privilege. Their meticulous scientific publications, with their rich illustrations and projections of the significance of these observations, form a continuing legacy for all future malacologists.

Key words: scientific contributions, prosobranchs, bivalves

Fields of scientific study are often strongly influenced by the activities of a few excellent practitioners. Their contributions serve as resources that build a foundation for future generations. Such is the case of the two scientists we celebrated at the World Congress of Malacology 2001 in Vienna. The field of study is functional morphology of molluscs, and the two scientists are Dr. Vera Fretter, University of Reading (UK), and Dr. Ruth D. Turner, Harvard University (USA). The symposium that follows, "New Frontiers in Functional Morphology of Molluscs" was organized by Dr. Shirley Baker (Florida State University at Gainesville) and Dr. Dianna Padilla (New York University at Stonybrook), and supported by the National Science Foundation and the American Malacological Society.

Common threads weave through the lives of these two superb scientists. First is the quality and excellence in their science, as seen in their careful and detailed observations of molluscs, plausible functional explanations of the morphological structures, and approaches to determine the connections between morphology and function. They both engaged in extensive fieldwork; their detailed observations, knowledge of living mollusks, and attention to all stages of their life cycles is reflected in their publications. Their publications are characterized by original drawings; the explanations are often connected to the evolutionary significance among the groups and have formed the basis for much of the research we now undertake in molluscan biology.

A second common strand is that Fretter and Turner have served as important role models for women and men who now study molluscs. Each scientist reflected a love of the organisms, attention to details, and unquenchable thirst to know what is inside of each animal and how it works. These characteristics have been passed on to many of the younger investigators.

Another thread is that these two women were very important among a group of functional morphologists, including Melbourne Carriker, Alastair Graham, Sir Maurice Yonge, Elizabeth Andrews, Brian Morton – to name a few, that are and were determiners of our understanding about evolution in the Phylum Mollusca. Today there is more emphasis on an experimental focus, on testable models with a biomechanical twist or a major ecological significance, and there are new tools available. Some of these tools are the use of endoscopy and high-speed video for non-invasive studies of such things as gill cilia feeding and monitoring internal currents; confocal microscopy with cellular markers to follow

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change in real time; genetic markers to address evidence of descent from common ancestors; computer models to generate and test ideas such as shell morphology; and scanning or transmission electron microscopy to increase our vision and look more closely at the insides and outsides of these molluscs. These studies, especially in the Prosobranchia and the Bivalvia, continue, as can be seen in the symposium presentations. We can be sure they are based on a firm scholarship when that foundation includes the publications of excellent functional morphologists like Fretter and Turner.

And a final thread is that these two women served as mentors for men and women around the world. They traveled to many countries at the invitations of colleagues at numerous colleges, universities, and world government organizations. Their passion and love for the molluscs and teaching were shared with many students in marine laboratories, field courses, and workshops; whether the students were young or old – they came away with a new appreciation for understanding the insides of molluscs and the functional significance of their structures.

Figure 2. Dr. Ruth D. Turner at the Woods Hole Oceanographic Institute (WHOI) being honored as the first woman to descend to the ocean floor in the WHOI Submersible RV *Alvin.* (WHOI photo)

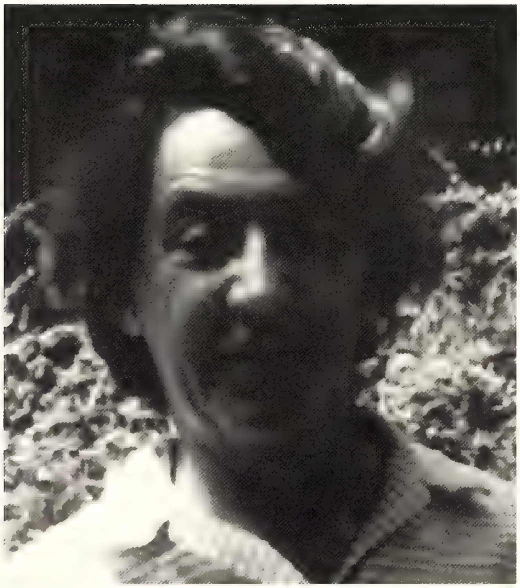

Figure 1. Dr. Vera Fretter at Reading University, taken in 1970. (Photo by M. Patricia Morse)

Figure 3. Dr. Ruth Turner at the Marine Science Institute in Nahant in 1969 with, left to right, Dr. Ken Boss, Dr. Gunnar Thorson and the author, Dr. M. Patricia Morse. (Photo by N.W. Riser)

DR. VERA FRETTER (1905 – 1992)

Dr. Vera Fretter (Fig. 1) began her career by attending a teacher's college and taught in a primary school. In a short time her interest in zoology prevailed and she entered Birbeck College in London, where she graduated with highest honors in Zoology in 1934. Under the tutelage of Professor Alastair Graham, she stayed on at the College to receive her Ph.D. two years later for her study on feeding and digestion in chitons (Fretter, 1937). She took a Lecturer position at Royal Holloway College, spending summers on the Cornish coast and continuing her studies, including a new interest in molluscan larvae. This was during World War II, and she related to the author that during one lecture, a bomb landed in the yard outside her window! She moved to the University of Reading, first as a Lecturer and then as a Reader, where she spent the rest of her career to retirement and beyond working on her molluscs, entertaining many visitors in her nearby home, and enjoying her beautifully kept garden. During her lifetime, Vera Fretter published over 80 papers, rich in observations and illustrations, on numerous prosobranchs, both adults and larvae. An account of her publications appears elsewhere in this volume (Padilla 2003).

It was during these years that the strong collaboration with Professor Alastair Graham was continued with numerous seminal publications including the well known and used volume *British Prosobranch Molluscs* (Fretter and Graham 1962, updated in 1994) and the teaching volume, *A Functional Morphology of Invertebrates* (Fretter and Graham 1976). The remarkable professional collaboration between Fretter and Graham was one of strong mutual respect and collective expertise, and the publications (often with Fretter's name first, and as Professor Graham noted to the author, "that is the way they are in the alphabet!") are numerous. For a more complete account of her contributions from the pen of Professor Graham, see Graham (1993).

Dr. Fretter reached beyond the University of Reading and its students in her influence on the study of malacology. She was a strong supporter of the Malacological Society of London. In addition, Dr. Fretter participated in post-graduate courses around the world. In 1965, as a member of the National Science Foundation Summer Institute on Marine Mollusca for graduate students at Coconut Island, University of Hawaii, she joined Drs. Alan Kohn, Martin Wells, and Alison Kay and introduced a number of our contemporary well-known molluscan biologists (for example, Geerat Vermeij and the late Richard S. Houbrick) to that inside world of molluscs. Vermeij (1997) notes in his autobiography (p. 83), "Vera Fretter from the University of Reading was one of the world's leading molluscan anatomists. With a wry sense of humor and frequent impish laughter, she set out to dissect all manner of snails."

A second course was given at the University of Southern California's Catalina Marine Station in 1970 (where I was privileged to teach with her). It was at the USC course that she met James McLean who, with a long history of expertise in molluscs, joined our course to learn more about the "insides" of molluscs. One outcome from this meeting was the series of papers on the vent limpets. Her work on these limpets, some of which measured only a couple of millimeters in length, forms a richly illustrated anatomical definition for these unusual species (Fretter *et al.* 1981, Fretter 1988, 1989, 1990). During the Catalina course Dr. Fretter asked if she might give a good number of the lectures, since at the University of Reading, Professor Graham usually did the molluscs! Her mentoring of my work while there on the functional morphology of the digestive system of *Pleurobranchaea californica* (Morse 1984) was a major change in my own understanding of how molluscs worked!

For several weeks in 1974 Dr. Fretter was a Visiting Professor at the Northeastern University's Marine Science Center in Nahant, Massachusetts. To sum up the impact that Dr. Vera Fretter had on those she met, I use the words of Professor Graham (1993), "Her enthusiasm and outgoing nature, her lively sense of humor, her great peal of laughter, made her welcome everywhere and not easily forgotten."

DR. RUTH DIXON TURNER (1914 – 2000)

Ruth D. Turner (Figs. 2, 3) began her career at Bridgewater State Teachers College, spent several years teaching high school, and then entered Cornell University, where she received an MS in Ornithology in 1944. Planning on a Ph.D. in Ornithology, she entered Harvard University. She soon was converted to the study of molluscs by Dr. William Clench, Curator of Molluscs, who became her Ph.D. advisor. After receiving a Ph.D. from Radcliffe College at Harvard University in 1954, Dr. Turner taught at Vassar College and then moved to Harvard University, where she was an Alexander Aggasiz Fellow and curator in Malacology from 1963 to 1975 at the Museum of Comparative Zoology (MCZ). In 1976 she was granted a full academic position as Professor in Biology at Harvard and continued her research at MCZ into the 1990s. One note in a publication citing her community leadership by the Harvard Community Resource (Early 1996) states, "Turner attributes much of her success at Harvard to Clench's modern attitude toward women and to his role as a friend and mentor." Dr. Bill Clench believed in the professional accomplishments of Ruth Turner, and remained her mentor, professional collaborator, and friend throughout his life. She was for many years a Curator in the Department of Molluscs, a mentor to endless students and colleagues, a teacher in courses at Harvard University, and author of numerous scientific articles. Malacologists throughout the world knew of her expertise and visited her laboratory. The United States Department of the Navy supported her work on wood boring bivalves for many years.

Dr. Turner introduced me to molluscs when I was in Graduate School at the University of New Hampshire. When I began teaching at Northeastern University, she gave me space at the MCZ at Harvard and introduced me to numerous scientists that passed through her laboratory. She was an ardent supporter of the Northeastern University Marine Science Center, where she would bring students to work on live animals, and visitors to see the Nahant rocky shore intertidal environment. As Amélie Scheltema of the Woods Hole Oceanographic Institute noted, "She opened doors for many and watched proudly as they started out their own careers" (Scheltema pers. comm.).

The major research contribution of Dr. Turner was the systematics, biology, ecology, and life histories of marine boring bivalves. Her early works on the systematics of molluscan groups often included detailed anatomical descriptions. A major contribution was the monograph on the family Teredinidae (Turner 1966). In the 1970s, she began studies on the life histories of wood-boring bivalves and joined forces with numerous post-doctoral associates at marine laboratories; they included active laboratories at Nahant, the Woods Hole Marine Biological Laboratory, and the University of Puerto Rico Marine Laboratory at La Parguera. Her work at the Woods Hole Oceanographic Institute was at the beginning of the deep-sea explorations. She was the first woman to dive on the WHOI deep-sea submersible ALVIN. Being first was not of great importance to Ruth Turner and she participated in about 20 such dives; what was important was the biology and life cycles of deep-sea molluscs. She wanted to know if boring bivalves would attack wood panels placed at these depths. In these latter experiments with wood panels in the deep sea she found rapid turnover of organisms – adding important new evidence that indicated rapid changes associated with ocean depths. Dr. Turner was also involved in describing the first deep-sea giant clam (Boss and Turner 1980). She continued her work on larval development associated with deep-sea molluscs, contributing pioneering work with Richard Lutz on modes of larval development at vent sites (Lutz *et al.* 1980, 1984, 1986, Turner and Lutz 1984). Dr. Turner published over 100 papers on molluscs.

In characterizing what Ruth Turner meant to one of the graduate students she mentored, I quote notes received from Dr. Elaine Hoagland (personal communication):

"Ruth Turner often said that she was one of the luckiest people alive, because she was paid to do exactly what she most wanted to do – research. She had an unquenchable curiosity and deep insight, combining traits usually reserved for the very young and very old. She also had a great practicality and confidence in her ability to get the data she needed to answer her research questions – hence she could invent new procedures and design equipment often 'on the spot' in the field, using the most basic of materials. She took her research wherever it led her, moving from taxonomy into ecology, physiology, and biochemistry, often through collaborations with colleagues and students. She was an awesome field worker because she lacked fear of physical challenges, even into her 80s. Ruth was patient, able to sit at a microscope or work on an anatomical drawing for hours. She was also intellectually modest, which made her a good listener." It could not be said any better!

Dr. Turner served the field of malacology in many ways; she was a member on 32 graduate student theses committees (both at Harvard University and around the world), participated in numerous workshops, and helped colleagues identify wood-boring bivalves in numerous field sites around the world. A large map in her MCZ office was covered with red tags indicating places she had visited and included stops on every major continent. She co-edited the MCZ monograph series *Johnsonia* and was president of the American Malacological Union and the Boston Malacological Society. Dr. Turner was honored by the Woods Hole Oceanographic Institution in 1996 as a "Woman Pioneer in Oceanography." Her own words indicate her timeless philosophy as recorded by Early (1996), " I always say to my students, 'Don't ever try to do something that doesn't interest you. If you do what you love, you'll succeed.' I've loved every minute I've spent with the biologists. I've enjoyed the privilege of these informal experiences. I've gotten paid to do the things I've most wanted to do. What more can you ask?"

SUMMARY

The scientific legacy of these two accomplished scientists continues in the timeless nature of their research on knowing about the nature of molluscs. The presentations of papers on functional morphology at this World Congress of Malacology attest to that importance. And perhaps as important is the active personal legacies these two "international treasures" left with those who were privileged to interact with them – to pass on the excitement and passion of discovery to the next generation of students who have a seed of wanting to know about molluscs.

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New frontiers in functional morphology of molluscs: A tribute to Drs. Vera Fretter and Ruth Turner

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Abstract: The symposium "New Frontiers in Functional Morphology of Molluscs" was held at the second World Congress of Malacology in Vienna, Austria, in August 2001. The symposium honored Drs. Vera Fretter and Ruth Turner, two outstanding women scientists who made significant contributions to the study of form and function of molluscs and played important roles in laying the groundwork for a growing field of research in functional morphology. The goals of the symposium were to focus attention on the vast potential of the use of molluscs as model systems in the study of form and function and to provide a forum for presenting new ideas and approaches and for proposing directions for future study. Symposium topics ranged from the processes of feeding in bivalves and gastropods to the biomechanics of byssal threads. These papers represent some of the diversity of research goals and methods in the field today and, it is hoped, will rejuvenate the field among the international community of malacologists.

Key words: Symposium, Form and Function

The study of form and function has been fundamental to the development of major areas of biological science, from medicine, physiology, and biomechanics, to ecology and evolution. The overwhelming complexity of bio study, presented obstacles to comprehensive understanding of function. Recently, important contributions to the understanding of functional morphology have been made by the comparative study of groups of organisms that are diverse but that share unifying structures at their basic levels of organization. One such group of model organisms is the phylum Mollusca.

Two women scientists, Drs. Vera Fretter and Ruth Turner, were pioneers, making significant contributions to the study of form and function of molluscs and playing important roles in laying the groundwork for this growing field of research. Both were also outstanding role models for women in science.

Dr. Vera Fretter (1905-1992) is best known for her outstanding contributions to our understanding of functional morphology of the "prosobranch" gastropods. She dedicated her career to understanding the relationships between morphology, function, and the fitness of species in different habitats. With her mentor, Alastair Graham, she produced the key reference on gastropods, *British Prosobranch Molluscs*, published by the Ray Society in 1962 and republished after her death (Fretter and Graham 1962, 1994). She published other key books on the functional morphology of molluscs and numerous papers on the biology, form, and function of a wide range of gastropods. In addition, she was a teacher and mentor to several generations of students, many of whom have become leaders in malacology. Dr. Fretter's life and scientific contributions have been summarized by Graham (1993), Chatfield (1993), and Morse (2003).

Dr. Ruth Dixon Turner (1914-2000) was the world expert on boring bivalve molluscs, the Pholadidae and the Teredinidae (shipworms). She was a dedicated teacher, a skilled dissectionist, and excellent illustrator. Dr. Turner was the first woman scientist to use the Deep Subermergence Research Vehicle ALVIN to study the deep sea and was honored by the Woods Hole Oceanographic Institution as a "Woman Pioneer in Oceanography." Her works include detailed descriptions of shipworm anatomy and boring, as well as notes on techniques in anatomical work and the use of cinephotomicrography in the study of form and function. Dr. Turner was an Honorary Life member of the American Malacological Union beginning in 1981 and served a term as Honorary President of the American Malacological Union (from 1997 until her death in 2000). Over the course of her career, Dr. Turner was a mentor to hundreds of students.

From the symposium "Frontiers in Functional Morphology" presented at the World Congress of Malacology, held 19-25 August 2001 in Vienna, Austria, and supported by the American Malacological Society and the National Science Foundation Ecological and Evolutionary Physiology Program (IBN-0090902).

Several authors have honored the life and contributions of Dr. Turner (Abbott 1973, 1987, Downing 1983, Boss 1989, Weber and Thurman 1991, Anonymous 2000, Buckley 2000, Mann 2000, Martin 2000, Morse 2003).

In 2001 a symposium at the second World Congress of Malacology (Vienna, Austria) was held not only to honor the past contributions and accomplishments of these two outstanding scientists, but also to look to the future. The following papers in this issue were inspired by this symposium.

An established researcher who knew Drs. Vera Fretter and Ruth Turner, M. Patricia Morse, started the symposium with a tribute to their lives and studies. This tribute was followed by contributions from younger scientists working in a variety of subdisciplines who have demonstrated the ability to take the field of molluscan functional morphology into innovative new directions. Our goal was to focus attention on the vast potential of the use of molluscs as model systems in the study of form and function by providing a forum for putting forward new ideas and proposing directions for future study. Symposium topics ranged from the feeding processes of bivalves and gastropods to the mechanical design of byssus, and served as the starting point for a lively discussion forum. These papers represent some of the diversity of research objectives and methods in the field today. Our hopes are that these contributions will draw attention to the study of functional morphology of molluscs and rejuvenate the field among malacologists.

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Nonoptimal shell forms as overlapping points in functional and theoretical morphospaces

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Abstract: Structural inefficiency for snail shells has been measured as the ratio of the volume of shell material : volume of space enclosed) (V_{shell}:V_{space}); however, whether structural inefficiency would be affected to a greater extent by varying V_{shell} or V_{space} (*e.g.*, by modifying whorl overlap) has remained uninvestigated. Structural inefficiencies for a variety of whorl overlaps were decomposed algebraically into V_{shell} and V_{space} and used to construct plots of whorl overlap and volume for 4 species of marine snails. Inflection points in those plots represent critical whorl overlaps beyond which space reduction starts to exceed significantly material conservation. Whorl overlaps that were obtained from measuring real specimens were less than whorl overlaps that were associated with inflection points, which indicates that living space might have predominated over shell material as a constraining factor during morphological evolution.

Key words: Graphical simulation, Mathematical model, Nonadaptive

In the subdiscipline of theoretical morphology known as theoretical conchology, mathematical models and computer graphical simulations are used to describe and depict real and hypothetical shell forms. Both shell form types can be represented as points within morphospaces, mathematical spaces wherein coordinate positions represent morphologies of organisms. As described by Hickman (1993a, 1993b) and Stone (1997a), morphospace types may be categorized by their delimiting axes: Axes for functional morphospaces may comprise anatomical, behavioral, ecological, or physiological parameters, whereas axes for theoretical morphospaces may comprise parameters in mathematical models that are used to describe forms.

The calcium carbonate structures that constitute the physical counterparts to computer graphics representing real shell forms (Douglas and Douglas 1985) provide barriers between internal soft bodies and external environments. Consequently, points representing real shell forms in functional morphospaces form subsets within regions containing points representing possible (*i.e.*, real and hypothetical) shell forms in theoretical morphospaces. These intersecting subsets constitute domains wherein shell structure may be analyzed from a conceptual perspective.

Shell structure inefficiency may be measured as the ratio of the volume of shell material : volume of space enclosed (V_{shell}:V_{space}). Considered exclusively in these terms, the optimal shell form for any species may be determined independently of the functions that shells serve. Deviations from optimality can be determined using analytical tools (*e.g.*, ontogenetic trajectory equations, computer graphics, and shell volume and surface area calculations) and used to test functional morphology hypotheses (*e.g.*, whether snails accrete real shells with optimal structural efficiency - *i.e.*, minimal structural inefficiency). In this symposium contribution, shell volume and surface area calculations and their application to functional morphology hypothesis testing are recapitulated, and plots of shell structure inefficiency are decomposed algebraically to determine whether space reduction or material conservation (or neither) predominantly affects the variation of structural inefficiency.

Shell volume and surface area calculations: Application to testing of functional morphology hypotheses

Calculations of shell volume and surface area probably were considered formally first by Moseley (1838), Canon Bristol and Natural History Professor at King's College in

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London. He derived equations for calculating volumes, surface areas, and other properties that characterize isometrically coiled shells; he revised those equations in 1842. Moseley was interested in buoyancies that are attainable by planispirally shelled cephalopods.

After a 99-year hiatus, Trueman (1941) developed more tractable but less accurate equations, using simplifying assumptions and an equation that was culled from Thompson's (1917, 1942) *Magnum Opus on Growth and Form*. Trueman was interested in locating centroids and determining buoyancies to deduce possible ammonoid life modes.

Less than a quarter-century later, Raup and Chamberlain (1967) published a paper in which they reported an error that they had identified in Trueman's (1941) formulation; they also reformulated and simplified Moseley's (1838, 1842) equations to provide alternatives. They proposed that these revised equations could be used to relate shell geometries and body chamber lengths or life position attitudes of ammonoids.

Five years later, Raup and (1972) published a paper in which they refined the geometric analysis that had been conducted by Raup and Chamberlain (1967). Raup and Graus derived equations to facilitate calculating coiled shell volumes and surface areas and suggested how these might be used to relate the efficiency of calcium carbonate utilization and ecological parameters in gastropods.

Two years later, Graus (1974) demonstrated that shallow-water marine gastropods exhibit latitudinal trends in their efficiency of calcium carbonate use and shell densities, thicknesses, and geometries. Because the solubility product for calcium carbonate decreases as temperature increases, the calcium carbonate that is available for shell construction in near-surface marine environments increases geographically from the poles to the equator.

Approximately one decade later, Heath (1985) used a geometric model to examine the extent to which whorl overlap determines shell structure inefficiencies for terrestrial snails (Fig. 1). Heath defined whorl overlap F as the proportionate loss from the diameter 2R for any circular aperture cross section with radius R that intersects with a previously existing circular aperture cross section with radius r (*i.e.*, $F = [R + r - d] / 2R$), wherein d is the vertical distance between circular aperture cross sections (Fig. 1, graphic at left). Heath quantified shell structure inefficiency using the quotient (P/A), where P and A represented, respectively, the noncontacting perimeter delineating the aperture with radius R and the nonintersecting area that is contained within it. Heath assumed that P was proportional to the surface areas of the shell material constituting whorls, whereas A was proportional to the volumes that were contained within them. Heath described F and (P/A) plots for models of slowly and rapidly expanding shell accretion modes and constant and variable interaperture areas, using parabolic curves (Fig. 1, graph at upper right). Because values of (P/A) that were obtained from real specimens exceeded minima of theoretical (P/A), which were calculated using real aperture radii but hypothetical whorl overlap ranges, Heath rejected the null hypothesis that terrestrial snails construct their shells with optimal efficiencies (*i.e.*, minimal shell structure inefficiencies). Also, because values of F that were obtained from real specimens exceeded those of F at minima of theoretical (P/A), Heath concluded that shells of terrestrial snails exhibit greater whorl overlaps than do hypothetical, optimally constructed shell forms.

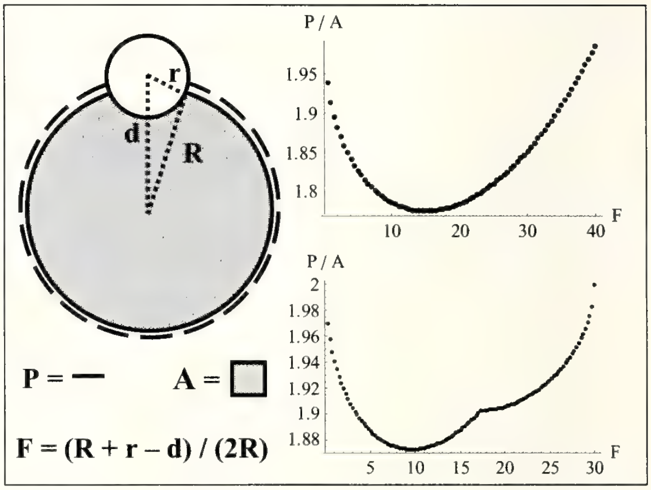


Figure 1. Geometric model (Heath 1985) and shell form inefficiencies (P/A) plotted against whorl overlaps (F). The variables P and A represent, respectively, the noncontacting perimeter delineating an aperture with radius R and the nonintersecting area A that is contained within it (graphic at left; apertures delimit a whorl and are separated by distance d; the previously existing aperture has radius r; whorl overlaps are quantified by F, which is dimensionless; P/A yields dimensional units length^{-1}). Data correspond to slowly and rapidly expanding shell accretion modes wherein $r = 0.9$, $R = 1.0$ units (graph at upper right) and $r = 0.3$, $R = 1.0$ units (graph at lower right).

After another decade had elapsed, Stone (1997b) presented a whorl-by-whorl method for calculating coiled shell volumes and surface areas, by combining allometry theory and the Theorem of Pappus (as described by Biddle [1984]). The Theorem of Pappus was proposed during the 3rd Century and rediscovered by Guldinus and demonstrated formally first by Cavalieri during the 17th Century. The theorem had been used implicitly in deriving equations for shell volumes and surface areas since Moseley (1838) published his classic paper, but Stone used it explicitly. Stone showed that volumes and surface areas that were calculated using the whorl-by-whorl method were more accurate than were those that were obtained using previously published equations, as those equations were formulated on the basis of an assumption that shells are accreted isometrically. However, Stone noted that the whorl-by-whorl method is more laborious and less elegant than are algebraic methods. Stone concluded that either approach may be adopted for shells exhibiting isometric variation, whereas the whorl-by-whorl method should be used for shells exhibiting allometric variation.

Two years later, Stone (1999) showed that plots of F and (P/A) for rapidly expanding shells with variable interaperture areas yielded curves that were similar to the smooth parabolas that had been presented by Heath (1985) but exhibited inflections, *i.e.*, curvature changes, at F characterizing real specimens (Fig. 1 herein, graph at lower right). Stone also incorporated shell thickness into the whorl-by-whorl method, so that shell material volumes could be calculated. Stone measured shell structure inefficiency using the ratio V_{shell}:V_{space}, wherein V_{shell} represented the volume of shell material and V_{space} represented the volume of enclosed space. Stone used a mathematical model and computer graphical simulation to depict for 4 marine snail species hypothetical shell forms representing possible whorl overlap ranges and calculated V_{shell}:V_{space} for each. Real specimens yielded nonoptimal V_{shell}:V_{space}, confirming Heath's conclusion that snails fail to achieve minimal shell structure inefficiencies. In particular, marine snail shells exhibited less whorl overlap than would hypothetical, optimally constructed shell forms. Stone also showed that whorl overlap and V_{shell}:V_{space} plots could be described accurately using polynomial functions (*i.e.*, quartic equations).

Hutchinson (2000) considered some inadequacies that are associated with adopting two-dimensional models to solve three-dimensional problems and re-examined analyses of whorl overlap and shell structure inefficiency. Hutchinson used the Theorem of Pappus to calculate shell volumes and surface areas and refined geometric analyses for shells that are accreted isometrically. In particular, he corrected the surface area equation that had been derived by Raup and Graus (1972), by accounting for whorl expansion (*contra* Hutchinson's claim that Stone [1997b] had overlooked whorl expansion, Stone explicitly implemented integration to calculate average perimeters and account for allometric aperture expansion). Hutchinson (1989) also rectified the uniform shell matrix secretion assumption that he and Rice (1998) had adopted previously, by accounting for differential accretion rates along the mantle edge.

Shell Structure Inefficiency Plots

The same conclusions that were drawn by Stone (1999), that snail shells exhibit less whorl overlap than would hypothetical, optimally constructed shell forms, may be drawn by fitting quadratic or cubic equations to {whorl overlap, V_{shell}:V_{space}} pairs (Fig. 2). As did the polynomial functions that were obtained by analyzing these data previously, cubic functions reveal inflection points. Stone suggested that inflection points on shell structure inefficiency plots (*e.g.*, those depicted by Stone (1999) and in Fig. 1 – graph at lower right and Fig. 2 herein) were intriguing because they could indicate critical whorl overlaps beyond which space reduction begins to

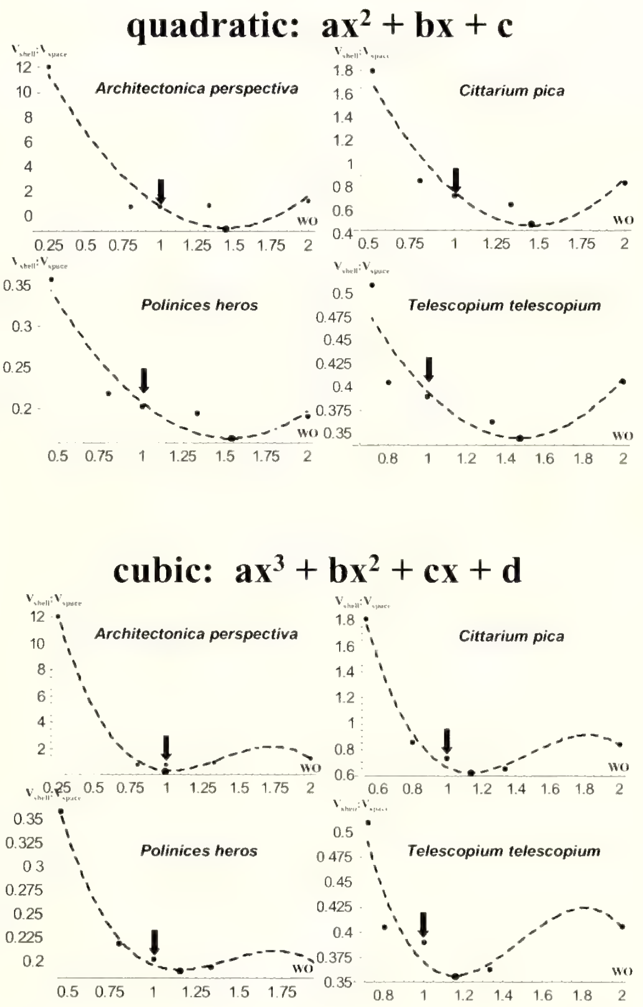


Figure 2. Whorl overlap WO and shell structure inefficiency (Vshell:Vspace) plots. The variable WO is measured relative to real specimens; Vshell represents the volume of shell material; Vspace represents volume of space enclosed (shell forms at WO = 1 represent real specimens; WO and Vshell:Vspace are dimensionless). Quadratic curves fitted to data (upper graphs) reveal that real specimens (for which WOs are indicated by arrows) exhibit less overlap than would hypothetical, optimally constructed shell forms (for which WOs are indicated by enlarged points). Cubic curves fitted to data (lower graph) also reveal that real specimens (for which WOs are indicated by arrows) exhibit less overlap than would hypothetical, optimally constructed shell forms (for which WOs are indicated by enlarged points).

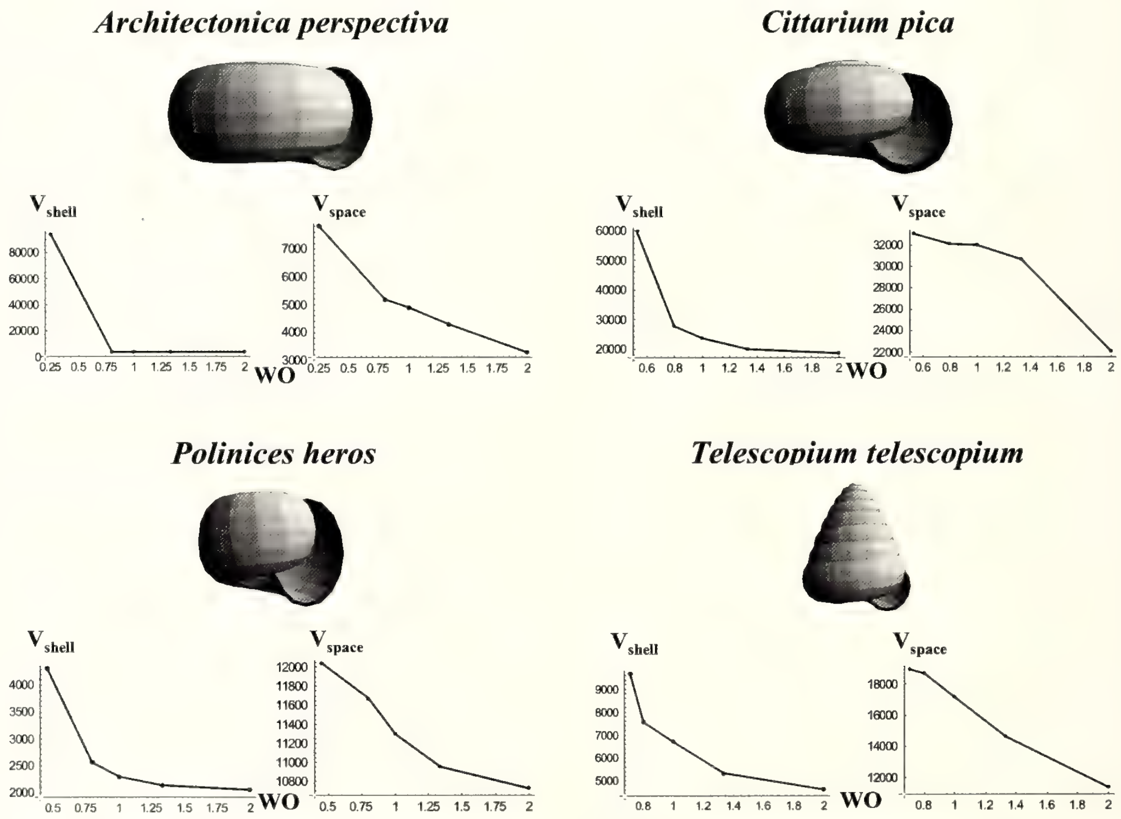
exceed significantly material conservation. That hypothesis is tested explicitly herein, by algebraically decomposing plots of shell structure inefficiency to compare the manner with which V_{shell} and V_{space} vary with whorl overlap.

METHODS

Plots of shell structure inefficiency for *Architectonica perspectiva* (Linnaeus, 1758), *Cittarium pica* (Linnaeus, 1758), *Polinices heros* (Say, 1822), and *Telescopium telescopium* (Linnaeus, 1758) that were published previously by Stone (1999) were decomposed algebraically into plots containing whorl overlap and V_{shell} and V_{space} . These species were chosen because they represent a spectrum, ranging from the small whorl overlap characterizing *T. telescopium* to the large whorl overlap characterizing *A. perspectiva*. Whorl overlap was defined with respect to actual whorl overlap (whorl overlap = 1 corresponded to actual shell forms) and altered by varying the translation parameter T in the mathematical shell model that is used in the computer program *CerioShell* (Stone 1995). The other three parameters, offset O, horizontal expansion H, and vertical expansion V, were fixed constant. Optimal shell forms for the 4 species were simulated graphically, using the technical computing environment *Mathematica* (Wolfram Research, Inc. 1988) as a software platform to run *CerioShell.*

RESULTS

In general, V_{shell} decreased substantially and then asymptoted with whorl overlap increases, whereas V_{space} diminished gradually and then decreased substantially (Fig. 3). The results



Architectonica perspectiva

Cittarium pica

Polinices heros

Telescopium telescopium

Figure 3. Optimal shell forms and plots of whorl overlap (WO) and volume (V) for 4 species of marine snail. The computer-generated graphics that are presented represent the optimal shell form for each species (for which WOs and shell structure inefficiencies may be gleaned from arrow locations in graphs in Fig. 2). Two graphs are presented for each species: the one on the left depicts a WO and the volume of shell material (Vshell) plot, the one on the right depicts a WO and the volume of space enclosed (Vspace) plot. In each plot, successive points are connected by straight lines (i.e., no mathematical model is fitted to the data) to facilitate gleaning variation (WO is dimensionless; volume units are mm^3).

that were obtained from analyzing *Cittarium pica* provided the most conspicuous instance for this trend, with an immediate decrease in V_{shell} and a delayed decrease in V_{space} (Fig. 3); similar but less conspicuous instances were obtained from the other species (Fig. 3). In all cases, actual specimen whorl overlap occurred at a relatively small whorl overlap (Fig. 2, arrows indicating whorl overlap = 1), where V_{shell} is decreasing substantially (Fig. 3, graphs at left); whereas the inflection point occurred at a relatively large whorl overlap (Fig. 2, enlarged points), where V_{space} starts to decrease substantially (Fig. 3).

DISCUSSION

After 164 years, accurate equations and methods for calculating isometrically and allometrically coiled shell volumes and surface areas are available for application to studies in functional morphology. Optimal shell construction can be analyzed using shell structure inefficiency plots, which may be described accurately with parabolic functions exhibiting inflection points (as shown previously by Stone (1999) and depicted in Fig. 1 - graph at lower right and Fig. 2 herein). These inflections can be reasoned intuitively. With no whorl overlap, a snail must accrete the entire surface for every whorl comprising its shell but can occupy an unimpeded space. With complete whorl overlap, a snail can utilize previous whorl surfaces in constructing subsequent whorls but must reside between the older and newer confines. Between these extreme situations, the relation between shell material that is used for construction and space enclosed that is available for living yields optima (*i.e.*, minima, as described previously by Stone (1999) and depicted in Fig. 1 - graph at lower right and Fig. 2 herein). Shell structure inefficiency plots are determined by differential variation between V_{shell} and V_{space}. This differential variation can be gleaned conveniently from plots of whorl overlap and volume (Fig. 3), which reveal that V_{shell} decreases substantially at small whorl overlaps, whereas V_{space} decreases substantially at large whorl overlaps. Thus, shell structure inefficiency plot inflection points represent critical whorl overlaps beyond which space reduction begins to exceed significantly material conservation (*i.e.*, material conservation begins to asymptote while space reduction begins to increase). On the basis of these observations, marine snail shells exhibit whorl overlaps that are nonoptimal (in structural efficiency terms) because they reside within a region in morphospace wherein the shell material that is used in construction is diminished (*i.e.*, their relatively small whorl overlaps are contained within domains over which shell structure inefficiencies are decreasing).

Stone (1999) proposed that the discrepancy between the greater-than-optimal whorl overlap that is exhibited by terrestrial snails, as identified by Heath (1985), and the less-than-optimal whorl overlap that is exhibited by marine snails, as calculated by Stone (1997b), might be attributable to the most obvious differences between their habitats. For example, calcium carbonate is more available in marine than in terrestrial environments, especially at low latitudes. The observation that V_{shell} effects greater variation in shell structure inefficiency than does V_{space} only for small whorl overlaps is consistent with this proposal: generally, because the building material (*i.e.*, calcium carbonate) is more abundant for marine snails, they effectively reside in more affordable dwellings in which taxes (*i.e.*, constraints that are associated with whorl overlap) are relaxed.

For any specific taxon, the theoretical morphology parameter of shell structure inefficiency is integrated with factors of functional morphology such as engineering principles (Curry 1970, Cain 1981), organic costs (Palmer 1992), fluid flow (Kitching *et al.* 1966, Garrity 1984, Denny 1988), predation (Vermeij 1976, 1987, Palmer 1979), and desiccation (Machin 1975) to effect shell forms. In this sense, nonoptimal shell forms represent the overlap between theoretical and functional morphologies.

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Mechanical design of mussel byssus: Load cycle and strain rate dependence

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Abstract: The ability to produce a strong byssal attachment is one key to the competitive dominance of mussels on many rocky shores. The byssus is composed of numerous extracellular collagenous threads, which in turn can be divided into proximal and distal regions that are distinct in ultrastructure and chemical composition. Our current understanding of the mechanical design of mussel byssus is largely based on quasi-static testing, where a fiber is slowly extended to failure. Mussels in nature, however, inhabit a dynamic environment where repetitive loads can be applied on short time scales. This study evaluates the mechanical properties of the threads of *Mytilus californianus* subjected to repeated subcritical loads and a range of strain rates. A subset of these mechanical tests was also performed on the threads of three other mytilid species. Results indicate that subcritical loading alters the mechanical properties of a thread in a manner that is dependent on the extension applied, and that thread stiffness and damping increase with increasing strain rate. Overall, this study provides insight into the mechanical design of a byssus that is subjected to dynamic loading.

Key words: *Mytilus*, byssal thread, modulus, strength, resilience

Mussels often dominate hard surfaces in temperate aquatic habitats, in part due to their ability to produce a strong attachment in the form of a byssus. Mussel byssus is composed of numerous byssal threads, each formed within a groove in the mussel foot by a process resembling polymer injection-molding (Waite 1992). The threads tether the mussel by providing the link between the substratum (via the adhesive plaque) and the stem/root system that is embedded in the byssal gland of the foot (Brown 1952; Fig. 1). The threads of mytilid mussels are extracellular collagenous fibers that can be divided into two distinct regions: (1) the corrugated *proximal* region, and (2) the smoother, narrower *distal* region that represents approximately two-thirds the total thread length (Bell and Gosline 1996).

The distinct ultrastructure and molecular composition of the two regions have been the focus of numerous studies (recently reviewed by Waite *et al.* 1998). The corrugated sheath of the proximal region covers loosely packed coiled fibrils, while the distal region contains dense bundles of filaments. Three collagenous proteins have been identified in the thread, each a natural block copolymer with a central collagen domain flanked by different domains: preCol P with elastin-like flanking

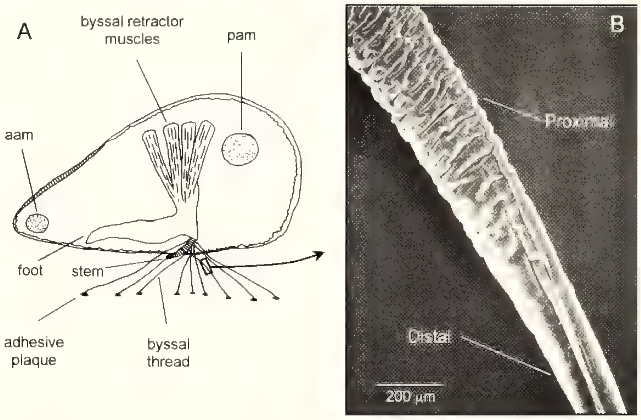

Figure 1. A. Anatomy of mussel byssus and musculature, adapted from Waite (1992). Approximate mussel shell length is 4 cm. Abbreviations: am, anterior adductor muscle; pam, posterior adductor muscle. B. Scanning electron micrograph of a portion of a *Mytilus californianus* thread, showing the transition from the corrugated proximal region to the smooth distal region.

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domains; preCol D with silk-like flanking domains; and preCol NG with glycine-rich, cell wall-like domains. PreCol P and preCol D predominate in the proximal and distal regions, respectively, while preCol NG is distributed evenly throughout the thread.

Given these disparities in composition and structure, it is not surprising that the two regions have been shown to differ in mechanical properties as well. Bell and Gosline (1996) extended earlier biomechanical studies (Allen *et al.* 1976, Smeathers and Vincent 1979, Price 1981) in detailing the low stiffness, low strength, and high extensibility of the proximal region in comparison to the distal region in three mytilids (*e.g.*, Fig. 2).

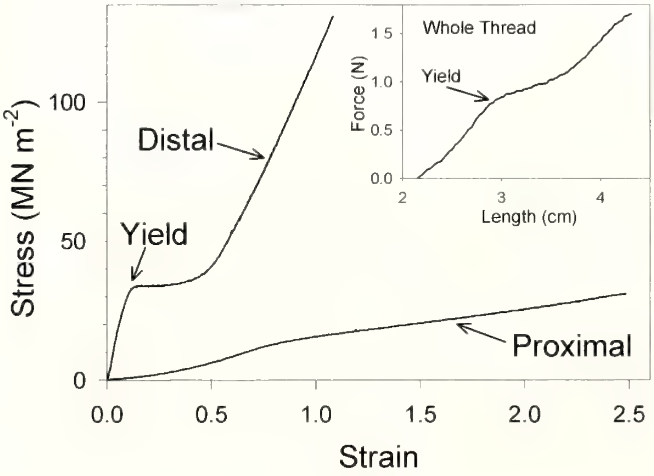

Figure 2. Representative tensile tests of two isolated regions and a whole thread (inset) of *Mytilus californianus*, after Bell and Gosline (1996). Note yield behavior of distal region is reflected in whole thread test. Extension rate = 10 mm min^{-1}.

Additionally, the distal region undergoes a distinct yield at approximately 20% extension, and then stiffens again before failure. The yield in the distal region plays the functionally important role of providing the extensibility needed to distribute an applied load over multiple threads, thereby increasing the strength of the entire byssus.

One limitation of these mechanical studies is that they involved quasi-static testing, in which threads were loaded to failure at relatively slow extension rates (5-25 mm min^{-1}, which corresponds to strain rates of 0.5-2.5 min^{-1} for a 10 mm sample). Wave-swept mussels, however, are likely exposed to more rapid, repeated loading regimes (applied over less than one second, Denny *et al.* 1998, Gaylord 1999, 2000). An interest in the dynamic mechanical properties of byssal threads has developed recently (Waite *et al.* 1998, Vaccaro and Waite 2001, Sun *et al.* 2001, Carrington 2002). These pioneering studies indicate that portions of mussel byssus exhibit the unusual properties of self-healing and strain-stiffening and may therefore provide insight into the design of novel polymers.

The purpose of this study is to provide a more detailed view of the dynamic mechanical behavior of byssal threads. By exposing whole threads and isolated thread regions to repeated subcritical loads and a range of strain rates, we demonstrate that subcritical loading alters the mechanical properties of byssal threads in a manner that is dependent on the amount of deformation that was applied. Furthermore, the overall stiffness and energy dissipation of byssal threads increases with increasing strain rate.

METHODS

Mytilus californianus Conrad, 1837 was the primary test species for this study, and all mechanical tests described here were performed on threads from *M. californianus*. A subset of these mechanical tests was also performed on other mytilids: *Mytilus trossulus* Gould, 1850, *Mytilus galloprovincialis* Lamarck, 1819, and *Mytilus edulis* Linneaus, 1758. With the exception of *M. edulis*, all animals were collected from Barkley Sound (48.8°N; 125.1°W) on the west coast of Vancouver Island, British Columbia, Canada. *M. edulis* was collected from Bass Rock in Rhode Island Sound (41.4°N, 71.5°W). Animals were maintained at 10-15°C in gently recirculating seawater for up to four months. Individual threads were carefully removed from their attachment points (the stem of the byssus and the substrate) and maintained unstretched in seawater until testing. Only one thread per individual was tested, either whole or only in the distal or proximal region. Each end of the sample was glued between two balsa wood tabs with cyanoacrylate and clamped within the testing apparatus. All mechanical tests were conducted in seawater at 15 ± 1°C.

Quasi-static testing

A tensometer was used to perform quasi-static testing, in which the force required to extend slowly a sample to a given length was recorded. An Instron-1122 tensometer was used for all tests, with modifications described by Bell and Gosline (1996), except for tests with *Mytilus edulis*, where an Instron-5565 equipped with a computer interface was used. Both tensometers were capable of a maximum extension rate of 1000 mm min^{-1}. When applicable, force measurements were converted to stress (σ, in N m^{-2}) by dividing by the cross-sectional area of the specimen. This area was assumed to be circular and was calculated from a sample diameter measured with an ocular micrometer (± 1 µm). Measurements of specimen length (l) were converted to strain (ε) using the formula $\varepsilon = (l-l_0)/l_0$, where l_0 is the initial unstressed length of the specimen. A strain value of 1 is equivalent to 100% extension, or a doubling of specimen length. Initial modulus (E_i) describes the stiffness of a material and is calculated as the slope (σ/ε) of the initial linear portion of a stress-strain curve.

Cyclical loading

A preliminary exploration of cyclical loading was first performed on whole threads from *Mytilus californianus*, in which a specimen was extended 5 mm min^{-1} to a subcritical length, returned to its initial length, and then extended to failure. A thread was cycled to one of two extensions: 11% (below the yield point) and 44% (well into the yield region). Data from the first cycle were used to calculate sample resilience, R, as the area under the return curve expressed as a percentage of the area under the extension curve. Resilience is a measure of elastic efficiency, or the percentage of elastic strain energy stored during deformation that is recovered in elastic recoil. Resilience is 100% for a perfectly elastic material, but is much lower for a material that dissipates strain energy through molecular friction (Gosline *et al.* 2002). Additionally, the percent change in initial modulus (0-11% extension) from the first to the second cycle was calculated.

More extensive mechanical tests were performed on whole threads cycled to 11% extension to evaluate differences among species and among stages of thread maturation (or "tanning"). First, laboratory produced threads of *Mytilus californianus*, *Mytilus trossulus*, and *Mytilus galloprovincialis* were tested, with sample sizes of 7, 12, and 3, respectively. All threads were 1-6 days old and were golden yellow in appearance. Analysis of variance was used to evaluate the effect of species on the change in initial modulus from the first to second load cycle. Second, whole threads of *M. californianus* at different stages of maturation were tested: milky white (< 24 hours old), golden yellow (1-6 days old), and dark brown (harvested in the field, age unknown). Sample size was 4, 7, and 12, respectively. Analysis of variance was used to evaluate the effect of thread maturation on the change in initial modulus from the first to second load cycle.

Cyclical loading was also performed on isolated distal and proximal regions of threads of *Mytilus californianus*. Distal regions were isolated from four separate animals and subjected to repeated cycles to four extensions: 8%, 16%, 35%, and 65%. Note that the first two of these extensions are below the yield point, the third is within the yield region, and the last is beyond the yield region. Resilience was calculated for the first cycle of each extension level.

Based on the results of these preliminary tests, the mechanical behavior of the distal region was explored in more detail using a time delay between extension cycles. Specifically, distal regions of the threads of *Mytilus californianus* were subjected to two extension cycles (either 35% or 65%), then left unstressed in 15°C seawater for 10 min, 30 min, 1 h, 16 h, 6 days, or 27 days. After the time delay, the two extension cycles were repeated. Three replicate distal samples were tested for each time delay, thus sample size was 18 for each of the two extensions. This protocol was also used for distal portions of the threads of *Mytilus edulis*, but only 35% extension cycles were performed and the 27-day treatment was omitted. Recovery of molecular structure in the distal region was calculated as the area enclosed by the force-extension loop after time delay expressed as a percentage of the area enclosed by the initial loop. Time values were log-transformed, and analysis of variance was used to evaluate (1) the effect of log-time and extension (35% *vs.* 65%) on the recovery of samples of *M. californianus* and (2) the effect of log-time and species (*M. californianus vs. M. edulis*) on the recovery of distal samples cycled to 35% extension (Systat version 10, Chicago, IL). Cyclical loading tests of proximal regions were less extensive overall; 7 specimens of *M. californianus* were cycled repeatedly to approximately 60% extension.

Strain rate dependence

Two methods were used to investigate the influence of strain rate on the mechanical properties of byssal threads from *Mytilus californianus*. The first method, performed only on paired samples from the same distal region, used the quasi-static tensometer (described above) at extension rates of 10 and 1000 mm min^{-1}. This method, while informative, was unable to achieve the extremes in extension rate that wave-exposed mussels are likely exposed to in nature (>> 1 cm s^{-1}, Denny *et al.* 1998) due to limitations of the tensometer.

The second method, dynamic testing, applied more rapid extensions to isolated proximal and distal regions, following the procedure of Lillie and Gosline (1990). Distal and proximal samples isolated from the same thread of *Mytilus californianus* were prepared for dynamic testing by subjecting the thread portions to twenty load cycles in the tensometer at an extension rate of 5 mm min^{-1}. Extensions were 50% and .5% for the proximal and distal regions, respectively, corresponding to loads of 0.1 to 0.2 N, and had the effect of stabilizing the mechanical behavior of the samples. Each sample was then mounted in the dynamic test apparatus and placed under a small, static load (0.02-0.05 N, below the yield point of a whole thread). Small amplitude, sinusoidal deformations were then applied to the samples at a range of frequencies (0-5 Hz, followed by 0-200 Hz). Spectral analysis of the resulting stress and strain waveforms provided two material properties for each frequency: (1) the dynamic modulus, E^* (in N m^{-2}), which is the ratio of the amplitudes of the stress and strain waveforms, and (2) δ, which is the phase shift between the two waveforms. The phase shift is generally reported as tan δ, and is an index of energy dissipation, or damping, of a material. Dynamic resilience can be calculated from these data using the formula: $R = e^{-2\pi \tan\delta}$ (Gosline *et al.* 2002). This equation reflects the full, sinusoidal deformation applied to the sample, but is not comparable to the resilience measured in quasi-static tests, because the latter most closely approximates a half cycle (a fiber cannot be compressed). Thus an alternative equation was used to calculate dynamic resilience per half cycle: $R = e^{-\pi \tan\delta}$.

RESULTS

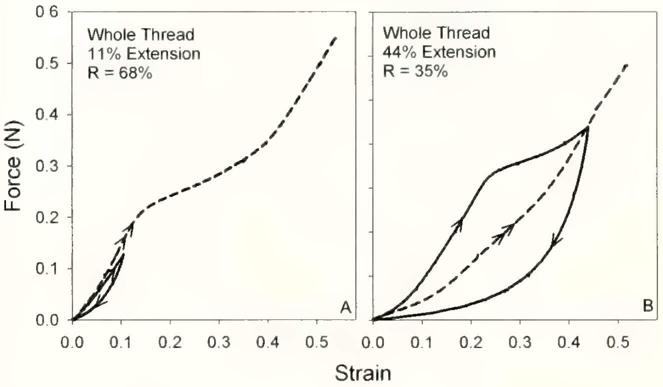

Figure 3. A single cycle of subcritical loading of whole threads of *Mytilus californianus* (solid line) followed by loading to failure (dashed line). A. Initial load cycle is below the yield strain (11% extension). B. Initial load cycle is beyond the yield strain (44% extension). Arrows indicate direction of loading; double arrows denote extension after initial cycle. Extension rate = 5 mm min^{-1}.

Cyclical loading

The mechanical behavior of whole threads depended on the extension to which they were cycled. The thread from *Mytilus californianus* shown in Fig. 3A was highly resilient (68%) when cycled to an extension below its yield point. When then loaded to failure, initial stiffness increased 22%, indicating that more force was required to achieve 11% extension. In contrast, the thread loaded beyond the yield point (44% extension, Fig. 3B), was much less resilient (35%) and a considerable amount of strain energy was dissipated in the cycle. When subsequently loaded to failure, the thread decreased in stiffness by 54% (measured over 0-11 % extension) and lacked a yield region.

Table 1. Change in initial modulus (stiffness) in whole threads of three *Mytilus* species cycled to 11% extension. Extension rate = 5 mm min^{-1}. SE = Standard error; N = sample size.

			% change in initial modulus		
Species	Age	Appearance	Mean	SE	N
M. californianus	1 – 6 days	Golden yellow	5.8	2.3	7
M. trossulus	1 – 6 days	Golden yellow	17.0	3.6	12
M. galloprovincialis	1 – 6 days	Golden yellow	17.9	5.0	3
M. californianus	< 24 hours	Milky white	14.1	2.1	4
M. californianus	Unknown (field-collected)	Dark brown	6.3	2.0	12

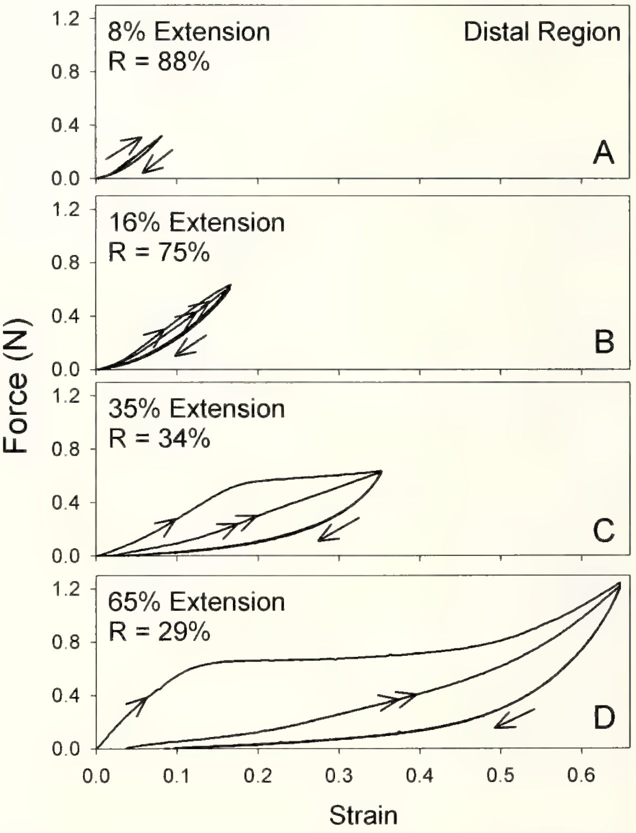

Figure 4. Cyclic loading of distal portions of byssal threads of *Mytilus californianus*, ranging from 8 to 65% extension (A-D, respectively). Arrows indicate direction of loading; double arrows denote second cycle extension. Resilience is calculated for first cycle only. Different threads were used for each extension, thus the first cycles do not overlap precisely. Extension rate = 5 mm min-^{1} for A and B; 10 mm min-^{1} for C and D.

The general trend of strain stiffening was observed in all threads cycled to 11% extension. The degree of strain stiffening in whole threads was indistinguishable among the three species tested (Table 1, golden yellow threads; F = 2.91, P = 0.08), and among the different stages of maturation (Table 1, *Mytilus californianus*; F = 2.73, P = 0.09). Note, however, that the statistical power of these analyses was low (0.31 and 0.34, respectively), due to sample size limitations.

Isolated portions of the distal regions of byssal threads of *M. californianus* also exhibited mechanical behavior that depended on the extension to which they were cycled. The distal region was stiff and highly resilient (88%) when cycled to a low extension (8%, Fig. 4A), and all subsequent cycles were indistinguishable from the first. When cycled to increasing extensions (16%-65%, Fig. 4B-D), the resilience of the first cycle decreased markedly (from 88% to 29%). Furthermore, the loading portion of the second cycle was less stiff than the first cycle, and this disparity increased with increasing cycle extension. The unloading (return) portions of the two cycles were identical for all extensions, and the third and all subsequent cycles were indistinguishable from the second cycles (data not shown).

The area enclosed by each force-extension loop represents the strain energy lost during deformation due to molecular friction. In previously unstressed, stiff threads cycled beyond their yield point, considerable energy was dissipated in the first cycle, but not in the second cycle (Fig. 5A). That is, the area enclosed by the second loop is only 38% of that enclosed by the first loop. Over time, however, the distal region began to increase in stiffness and recover the energy dissipating behavior of the first cycle. For example, when left unstressed for 30 minutes and then cycled twice, the area enclosed by the first force-extension loop at t = 30 min was 68% of the first cycle at t = 0. The subsequent cycle then reverted to a loop similar to the second cycle at t = 0.

The area enclosed by a force-extension loop after a time delay expressed as a percentage of the area enclosed by the initial loop provides an index of "recovery" of molecular structure in the distal region. In threads from *Mytilus californianus*, recovery increased as a logarithmic function of time (F = 464.7, P < 0.001) and depended on the extension that was applied (F = 24.9, P < 0.001; Fig. 5B). The interaction between log time and extension was not significant (F = 0.8, P = 0.37), thus threads cycled to 65% extension recovered at the same rate, but took longer to achieve a given level of recovery because they exhibited a greater initial loss of stiffness. Only 50 - 60% recovery was achieved in 30 minutes, and full recovery required several weeks. The general behaviors of the load cycles were similar for distal portions of threads of *Mytilus edulis*, but the rate of recovery at 35% extension was reduced in comparison to those of *M. californianus* (species x log time interaction, F = 8.5, P < 0.01; Fig. 5B).

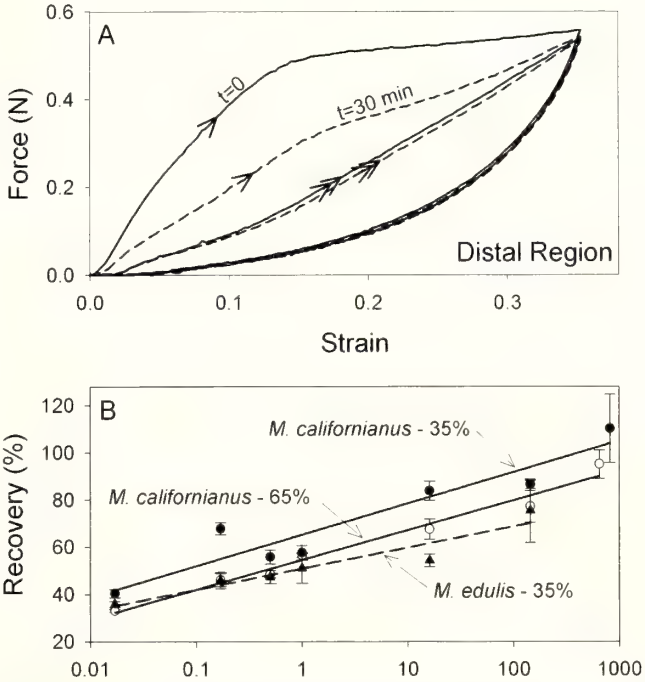

Figure 5. Cyclic loading of the distal portion of a byssal thread with a time delay. A. Representative test of a thread from *Mytilus californianus* loaded to 35% extension. Two cycles were conducted at t = 0 (solid lines), followed by two more cycles after a 30 minute delay (dashed lines). The area enclosed by each force-extension loop represents the strain energy lost due to deformation. Adapted from Bell (unpublished data) in Waite et al. (1998). B. Recovery of energy dissipation in threads of *M. californianus* (loaded to 35% and 65% extension, solid and open circles, respectively) and *Mytilus edulis* (loaded to 35% extension only, triangles) as a function of time. Recovery was calculated as the energy dissipated at time t divided by the energy dissipated at time t = 0 (see text for details). Symbols are mean values ± SE, n = 3. Extension = 10 mm min^{-1}.

Isolated portions of the proximal regions of the byssal threads of *Mytilus californianus* were highly variable in mechanical behavior when cycled. Many thread samples increased in stiffness when cycled; an extreme example of this behavior is shown in Fig. 6. This sample, taken from an unstressed thread produced in the laboratory, initially increased in stiffness and resilience with each successive cycle. The material stabilized after approximately 15 cycles, with an overall 80% increase in stiffness and 60% increase in resilience compared to the first cycle. Cyclical loading of the other samples exhibited only modest stiffening, or none at all (data not shown).

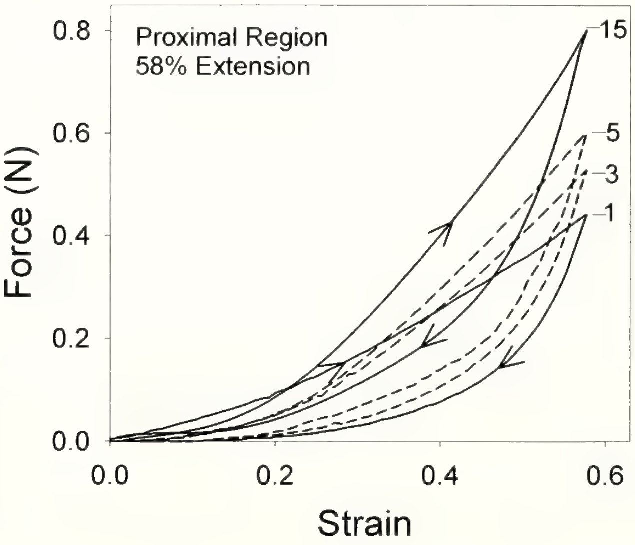

Figure 6. Cyclic loading of proximal region of a byssal thread. This thread from *Mytilus californianus* was cycled fifteen times to 58% extension at a rate of 5 mm min^{-1} (only cycles 1, 3, 5, and 15 are shown for clarity). Resiliences for cycle 1 and 15 are 42% and 67%, respectively.

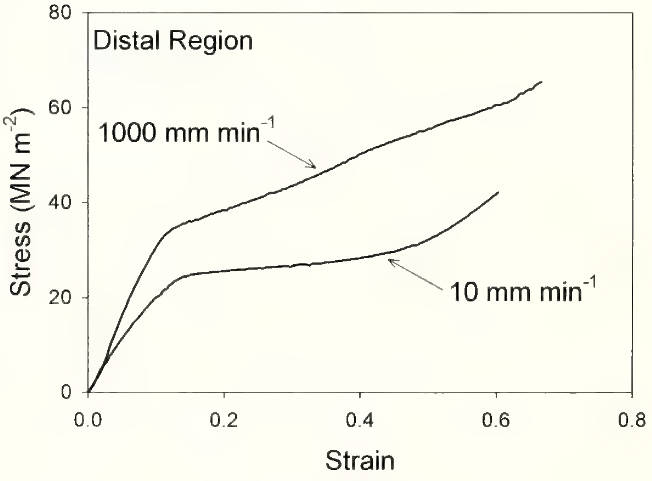

Figure 7. Mechanical testing of the distal region of a byssal thread at two extension rates, 10 mm min^{-1} and 1000 mm min^{-1}. Samples were taken from the same thread of *Mytilus californianus*. Both samples failed at one of the grips, thus these tests underestimate the ultimate properties of the samples.

Strain rate dependence

The mechanical behavior of byssal threads also depended on the rate at which they were extended. When a distal region was divided into two samples, each tested at a different extension rate, the sample strained at the higher rate exhibited increased stiffness and yield stress. For the thread shown in Fig. 7, the sample tested at 1000 mm min^{-1} was 60% stiffer and yielded at a 40% higher stress than the sample tested at the slower extension rate. The yield strain remained unchanged, and the yield "plateau" was less distinct at the higher extension rate. Unfortunately, grip failures were very common with this protocol and it was not possible to evaluate the effect of strain rate on ultimate properties of the distal region.

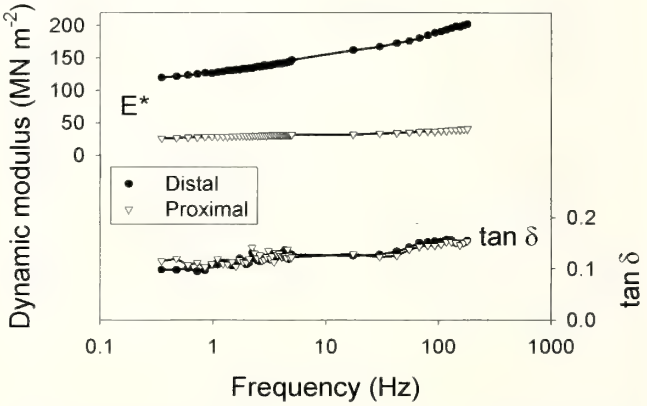

Figure 8. Dynamic mechanical properties of proximal and distal regions from the same byssal thread of *Mytilus californianus*. Static load was 0.022 N and 0.046 N for proximal and distal regions, respectively. Data were smoothed with a five-point running average; only every fifth point is plotted.

The dynamic moduli of isolated regions of byssal threads increased with increasing frequency (Fig. 8). Over three decades of frequency, the dynamic modulus, E*, ranged from 27 to 41 MN m^{-2} in the proximal region, and from 120 to 202 MN m^{-2} in the distal region. Tan δ also increased with test frequency, ranging from 0.10 to 0.15 for both thread regions, and dynamic, half-cycle resilience ranged correspondingly from 97% to 62%.

DISCUSSION

This study demonstrates that the mechanical behavior of mussel byssus described in quasi-static studies (e.g., Smeathers and Vincent 1979, Bell and Gosline 1996) is not fixed, but instead depends on the loading history of the thread. In *Mytilus californianus*, whole threads cycled below the yield point were highly resilient and increased slightly in stiffness when loaded once again. This strain-stiffening behavior did not depend on the maturation of the thread, and has also been observed in *Mytilus trossulus* and *Mytilus galloprovincialis* (this study) and *Mytilus edulis* (Carrington 2002). In contrast, threads cycled beyond the yield point had much lower resiliency and were dramatically less stiff when reloaded. These unusual behaviors are due to the load cycle dependence of the two components of the threads, the proximal and distal regions.

At low extensions, the strain-stiffening behavior of whole threads was solely due to the properties of the proximal region, where stiffness and resilience can increase dramatically upon cycling. The distal region was very stable at these extensions, and because the proximal region is the smaller portion of the thread (20-40%), the strain-stiffening effect in whole threads was less dramatic. Cycled proximal regions eventually stabilized and began to exhibit more characteristic stress-softening behavior (deforming slightly with each successive cycle). We observed that the number of cycles required to achieve this state was highly variable among "virgin" threads that were recently produced in the laboratory (1-6 days old). Sun *et al.* (2001) explored the molecular basis of irreversible strain stiffening in the proximal region of byssal threads of *M. galloprovincialis*, demonstrating that it can be achieved by aeration and prevented by oxygen depletion in the absence of mechanical loading. While this clever observation provides invaluable insight into the biomolecular structure of this material, it is difficult to imagine how it might apply to mussels that typically inhabit well-stirred and aerated environments in nature. Indeed, we observed strain stiffening behavior in both threads that were young (milky white) and well-aged (tanned) in the field. Thus the process and functional importance of strain stiffening in naturally occurring byssal threads remains unclear.

The loss of resiliency and stiffness in whole threads cycled beyond the yield point was due to the properties of the distal region, which exhibits stable, highly resilient cycles when loaded below the yield point. When loaded beyond the yield point, the distal region deformed and dissipated energy via molecular friction. In the short term (minutes), the region remained deformed and subsequent cycles exhibited low stiffness and only modest energy dissipation. In the long term (days), the deformation was reversible and the distal region recovered to a stiff, energy-dissipating fiber. This ability to "self-heal" (*sensu* Vaccaro and Waite 2001) was dependent on the amount of deformation applied, with greater deformations requiring a longer recovery.

For a given extension, self-healing was more rapid in threads from *Mytilus californianus* in comparison to *Mytilus edulis* (this study) and *Mytilus galloprovincialis* (Vaccaro and Waite 2001). These results extend the observations of Bell and Gosline (1996, 1997) that threads of *M. californianus* outperform those of "*edulis*-like" species (*M. edulis*, *M. galloprovincialis*, and *M. trossulus*; McDonald and Koehn, 1988) in stiffness, extensibility, and thickness. The inferior threads of "*edulis*-like" species are not necessarily maladaptive, since these mussels typically inhabit calmer shores and have "weedy" life histories (rapid growth, early reproduction) that may compensate for a weaker mechanical design (Koehl 1999). Threads of *M. californianus* and *M. edulis* differ in amino acid composition (Mascolo and Waite 1986), but the biomolecular basis for the superiority of *M. californianus* threads (particularly in the distal region) is at this point unknown.

Mussels living on rocky shores are subjected to dynamic loading by waves arriving approximately every ten seconds (Denny 1988). Because waves often travel in "sets," extreme forces on mussels are likely generated in rapid succession, on a time scale of seconds to minutes. If a single wave is large enough to load a thread beyond its yield point, the thread is able to dissipate much of that energy via deformation in the distal region. But full recovery from this deformation is quite a slow process, and the thread will certainly face the next wave with compromised stiffness. The remaining threads would then follow the same process in subsequent waves. Although the strength of each individual thread remains unaltered, such a reduction in thread stiffness reduces the overall attachment strength of a mussel (~20%; Bell and Gosline 1996). Thus it appears that mussels should avoid loading individual threads beyond their yield point, and Bell and Gosline (1996) suggest that this is exactly what they do: the estimated stress per individual thread for a typical wave falls well below the yield stress for *Mytilus californianus*.

The discussion above is based on mechanical tests performed at slow strain rates that are not characteristic of the rapid loading to which wave-swept mussels are subjected in nature (Denny *et al.* 1998, Gaylord 1999, 2000). Distal regions of byssal threads of *Mytilus californianus* are stiffer and yield at a higher force when strain rate is increased. Similar observations have been made for the distal regions of threads from *Mytilus galloprovincialis* (Vaccaro and Waite 2001). Dynamic tests indicated that both the proximal and distal regions of the threads of *M. californianus* increased in stiffness and became less resilient with increasing test frequency, suggesting that whole threads do as well. According to the model of Bell and Gosline (1996), increased stiffness and yield force in individual threads would enhance the strength of the entire byssus. Thus mussels exposed to rapid loading may have increased attachment strength in comparison to mussels that are loaded slowly.

This study furthers our view of the mechanical design of mussel byssus by considering the dynamic environment in which mussels live. While the dynamic mechanical properties of byssal threads have by no means been characterized completely, unique properties have been identified and provide an enhanced framework for biomolecular studies aimed at improving the design of man-made fibers (*e.g.*, Vaccaro and Waite 2001, Sun *et al.* 2001), and for ecomechanical studies that explore the hydrodynamic loading of flexible, wave-swept organisms (e.g., Denny *et al.* 1998).

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Functional anatomy of feeding in *Psiloteredo healdi* (Teredinidae): How the animal handles two discrete food sources

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Abstract: We used SEM and traditional light microscopy to investigate how the teredinid bivalve *Psiloteredo healdi* deals with wood particles entering via the pedal opening and suspended material entering via the incurrent siphon. The routes of these two food sources are partially segregated by the main bulk of the visceral mass, which greatly restricts the anterior third of the mantle cavity. Small particles of wood removed by drilling action of the shell are transported by ciliated tracts on the pedal surface to the mouth or to mantle tracts for rejection. Alternating areas on the foot surface with and without cilia suggest that expanding and retracting the foot can control the flux of wood particles. The very elongate body region posterior to the shell houses the main regions of the ctenidia responsible for the primary size-selection of suspended particles. Mantle tracts capture and remove excess wood and suspended matter to be discarded as pseudofeces. This is the first study to use SEM to analyze the organs and structures of the mantle cavity in a teredinid. SEM images allowed precise identification of the different types of cilia and their distributions in the epithelia of the mantle, palps, foot, and ctenidia.

Key words: Scanning Electron Microscopy, mantle cavity, morphology

The Teredinidae is a family of highly specialized bivalves that drill into and make tunnels in wood. They feed on wood scraped from the anterior blind end of the tunnel and on suspended particles entering via the posterior incurrent siphon. Despite the extensive literature on Teredinidae, little is known about their functional anatomy. The only studies on this subject are those of Atkins (1937), Purchon (1941, 1960), Morton (1970, 1978), Basylinsky and Rosenberg (1983), Martinez (1987), Martins-Silva (1997), Lopes and Narchi (1998), and Lopes *et al.* (1998, 2000).

Studies on the functional anatomy of Teredinidae have been based on light microscopic examination of the organs and structures. Only a few studies of this family have used scanning electron microscopy (SEM) (*e.g.* Basylinsky and Rosenberg 1983, Fuller *et al.* 1989, Tan *et al.* 1993, Lopes *et al.* 2000), even though this technique has been widely used to understand the structure and function of organs in other Bivalvia.

Lopes *et al.* (2000) analyzed the functional anatomy of the digestive system of *Psiloteredo healdi* (Bartsch, 1931), focusing on food processing after ingestion. In the present study, we show how this hermaphroditic species handles food in the mantle cavity prior to ingestion. By using SEM and observing the movements of particles in living animals, we determined the different types of cilia, their distributions in the epithelia of the mantle, foot, palps and ctenidia; and the ciliary currents related to selective food capture and particle elimination. This is the first study to use SEM to analyze the organs and structures of the mantle cavity in a teredinid. This technique allowed us to visualize the complexity of ciliation in *P. healdi*, and to hypothesize how the animal deals with two distinct types of food: wood and suspended particles.

MATERIALS AND METHODS

Psiloteredo healdi was collected in Rio Comprido, São Paulo State, Brazil (22°30'S; 45°15'W) in submerged logs from brackish to almost fresh water. Logs were kept in aquaria at a salinity of 10‰. More than 100 living and fixed specimens, ranging from 5 to 15 cm in length, were analyzed for the present study.

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Ciliary currents were observed on live, dissected specimens with carmine, Acquadag (a colloidal graphite), carborundum grade F3 particles, or fine sawdust fragments placed directly on the organs of the bivalve. Most often each type of particle was released independently over the surface of the organs and structures as a surrogate for the suspension coming from the water outside the tunnel. Particles were also released over the pedal surface as a surrogate for the wood drilled by the cutting action of the shell at the dead end of the tunnel.

Specimens were relaxed in cold water (4°C) overnight before being fixed for scanning electron microscopy (SEM). Foot, mantle, ctenidia, and palps were prepared for SEM according to the methods described by Leonel *et al.* (1998) with some modifications. The material was prefixed in 3% glutaraldehyde buffered with 0.2M cacodylate at 4°C overnight and washed in distilled water for 30 minutes. Excess mucus was removed by submerging the material in distilled water and submitting it to ultrasound for 2 minutes. The tissues were then postfixed at 4°C for an hour in 1% osmium tetroxide, washed in distilled water, and transferred to 1% tannic acid for 20 minutes. After being washed in distilled water the material was dehydrated in a graded ethanol series and critical-point dried.

RESULTS

General Anatomy of the Organs in the Mantle Cavity

The elongated main bulk of the visceral mass greatly restricts the anterior third of the mantle cavity of *Psiloteredo healdi*. The remaining two thirds, however, is broad and only occupied by the posterior regions of the ctenidia (Fig. 1). Each ctenidium consists of only one demibranch, and, as in most Teredinidae, is divided into three regions: the anterior and posterior, each with filaments and marginal food groove, separated by an intermediate region restricted to the food groove (Fig. 1). The labial palps are very reduced. The dorsal palps have expanded free distal ends. Each ventral palp is reduced to a slender, low epithelial fold. The foot, which lies at the anterior end of the body, is very reduced and has the same structure as in other Teredinidae (*e.g.*, Turner 1966, Lopes and Narchi 1998).

Mantle

At the anterior region of the body the mantle secretes the very reduced shell, while at the posterior region it produces a pair of calcareous pallets that control the opening/closure of the animal's tunnel. Between these extremes the external epithelium of the mantle is protected by a thin calcareous tube that it secretes against the wall of the tunnel in the wood.

The mantle collar surrounds the bases of the siphons and pallets (Fig. 1). On each side of the body, just anterior to this collar, the external surface of the mantle exhibits a U-shaped area corresponding to the origins of the protractor muscle of the pallets and retractor muscles of the siphons that are fixed on the calcareous tube. A special mantle gland (Sigerfoos 1908, Lopes and Narchi 1998) is visible as a globular corpuscle immersed in the connective tissue of the mantle, between the left and right U-shaped areas, in a median dorsal region (Fig. 1).

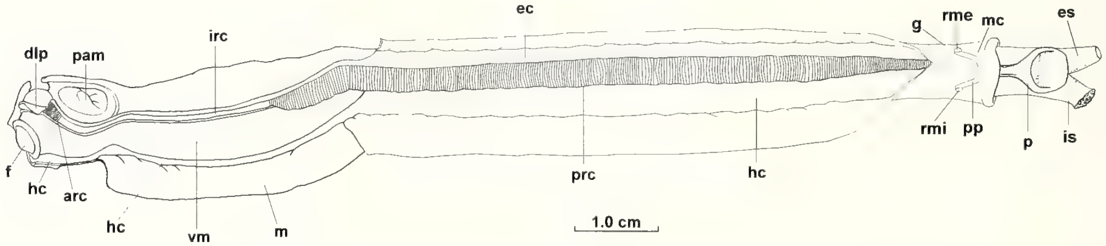

Figure 1. Diagram of the body (left view) of *Psiloteredo healdi* after removal of the shell, with the mantle sectioned longitudinally and deflected to show the organs of the mantle cavity. Abbreviations: arc, anterior region of the ctenidium; dlp, dorsal labial palp; ec, epibranchial cavity; es, excurrent siphon; f, foot; g, special mantle gland; hc, hypobranchial cavity; is, incurrent siphon; irc, intermediate region of the ctenidium; m, mantle; mc, mantle collar; p, pallet; pam, posterior adductor muscle; pp, protractor muscle of the left pallet; prc, posterior region of the ctenidium; rme, retractor muscle of the excurrent siphon; rmi, retractor muscle of the incurrent siphon; vm, visceral mass.

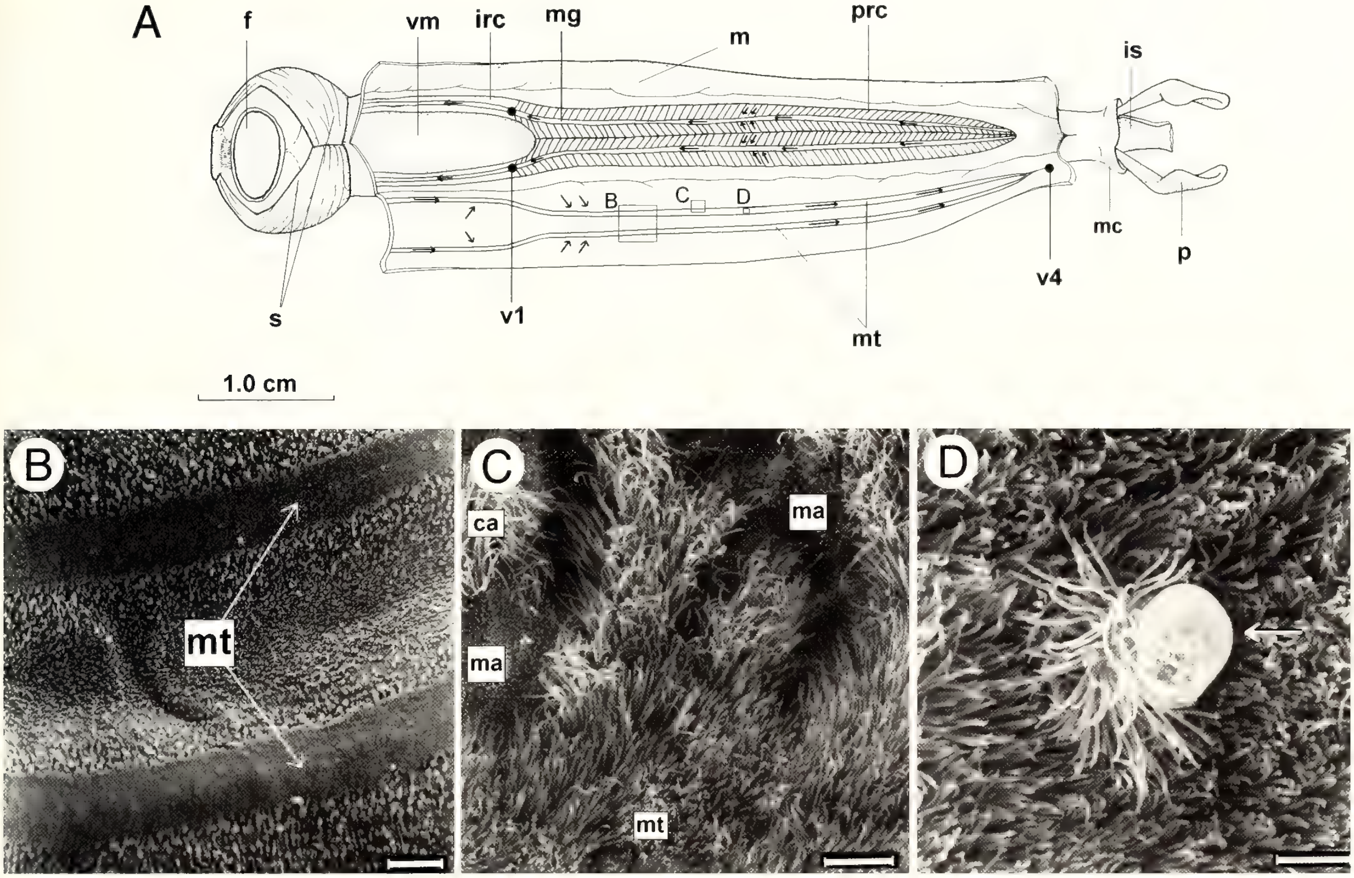

Figure 2. A. Diagram of the body of *Psiloteredo healdi* in ventral view, with the mantle sectioned longitudinally along the left side and deflected to the right to show ciliary currents on the ctenidia and internal mantle epithelium. Arrows pointing to the left show ciliary currents processing suspended material on the posterior and intermediate regions of the ctenidia. Arrows pointing to the right show cleansing currents on the mantle dealing with unwanted or excess suspended and wood particles. Squares labeled B, C, D indicate regions illustrated in SEMs B, C, D. B. SEM of the two parallel longitudinal ciliated rejection tracts and adjacent epithelium. Scale bar = 200 µm. C. Detail of the internal mantle epithelium showing ciliary areas intermingled with non-ciliated, microvillar areas. Scale bar = 10 µm. D. Detail of a longitudinal rejection tract showing a vesicle of mucus (arrow). Scale bar = 5 µm. Abbreviations: ca, ciliary areas; f, foot; irc, intermediate region of the ctenidium; is, incurrent siphon; m, mantle; ma, microvillar areas; mc, mantle collar; mg, marginal food groove; mt, longitudinal, ciliated rejection tract of the mantle; p, pallet; prc, posterior region of the ctenidia; s, shell; v1, vortex between posterior and intermediate regions of the ctenidia; v4, vortex at the base of the incurrent siphon; vm, visceral mass; •, vortex where particles converge.

The internal epithelium of the mantle has scattered gland cells and is ciliated throughout its extent. SEM revealed that cilia are not uniformly distributed. Two densely ciliated longitudinal tracts, each about 200 µm wide, are present near and equidistant from the median ventral line of the hypobranchial cavity (Fig. 2A, B). These tracts extend from the vicinity of the labial palps to the base of the incurrent siphon, where they fuse together and extend slightly into the siphon. The internal epithelium of the mantle, adjacent to the ciliated rejection tracts, is also ciliated, but the cilia are grouped in tufts separated by non-ciliated microvillar areas (Fig. 2B, C). The cilia of these tufts are similar to those of the longitudinal tracts. Spheres of mucus were detected along those rejection tracts (Fig. 2D).

Foot

The foot of *Psiloteredo healdi* (Figs. 1-3) is very short, even when fully protracted. Its distal region is discoid and separated from the proximal cylindrical region by a deep ring-shaped groove (Fig. 3A). The foot surrounds the crystalline

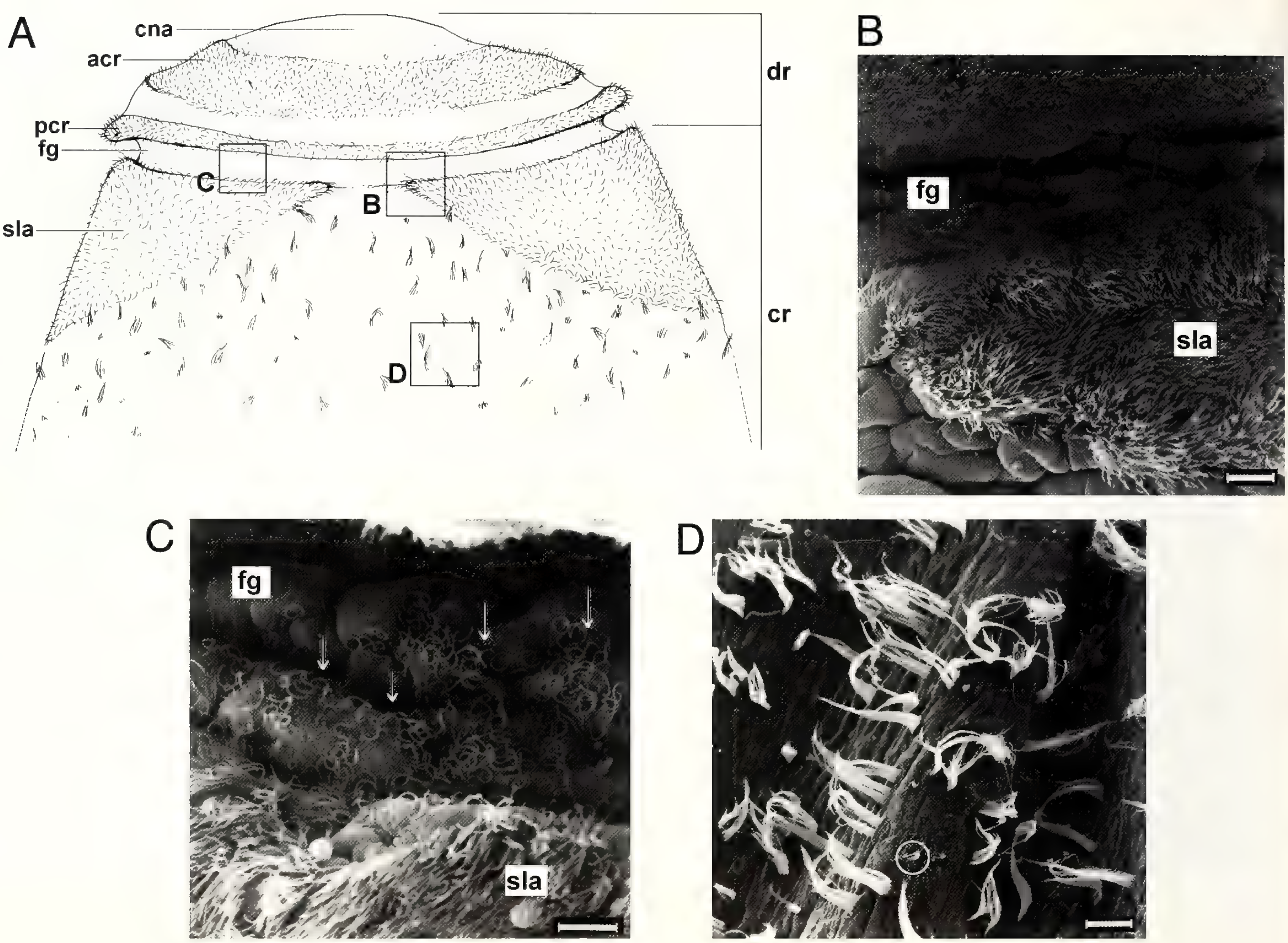

Figure 3. A. Diagram of the relaxed foot of *Psiloteredo healdi* in ventral view to show the discoid and cylindrical regions and their ciliated areas. Squares labeled B, C, D indicate regions illustrated in SEMs B, C, D. B. Detail of a portion showing the non-ciliated, ring-shaped foot groove and a corner of the densely ciliated semi-lunar area. Scale bar = 10 µm. C. Free microorganisms in the ring-shaped foot groove (arrows). Scale bar = 10 µm. D. Sparse flame-like tufts of long, thin cilia (approximately 30 µm long) of the epithelium lining the cylindrical region between the ciliated semi-lunar areas. The circle surrounds a tuft of shorter (approximately 2 µm long) cilia also found in this region. Scale bar: 15 µm. acr, anterior ciliated ring-shaped area; cna, central, non-ciliated area; cr, cylindrical region; dr, discoid region; fg, foot groove; pcr, peripheral ciliated ridge; sla, semi-lunar area.

style sac. When the foot contracts, the well-developed, rigid, crystalline style presses against the discoid region, making it convex.

The presence of cilia on the pedal epithelium was observed with light microscopy, but only SEM revealed that these cilia vary in size, arrangement, and distribution. In addition, SEM allowed us to understand how the cilia deal with wood particles. The central portion of the discoid region of the foot is lined by a non-ciliated epithelium and is surrounded by a densely ciliated ring-shaped area (Fig. 3A) bearing short cilia (about 5 µm long) with uniform diameter. Tufts of three or more cilia, each about 10 µm long, occur at the periphery of the central, non-ciliated area. Each cilium in the tuft gradually decreases in diameter toward the apex. A ring-shaped, non-ciliated area separates the preceding ciliated ring from a densely ciliated ridge (cilia about 5 µm long and uniform diameters) located just at the periphery of the discoid region of the foot. The groove separating the anterior discoid from the posterior cylindrical regions of the foot has no cilia (Figs. 3A-C). A well-defined, densely

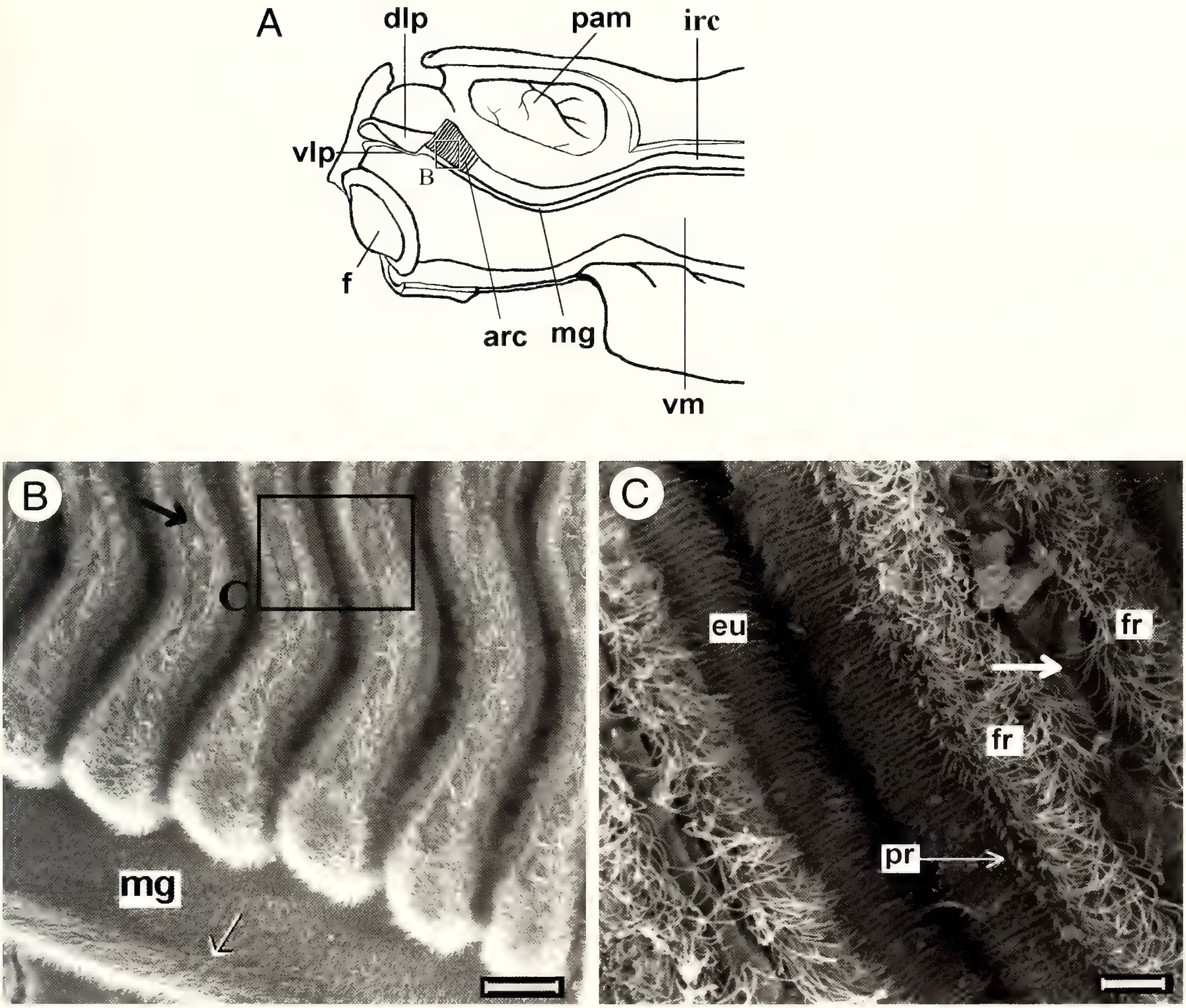

Figure 4. A. Diagrammatic representation of the anterior region of the body of *Psiloteredo healdi* after removal of the shell valves and mantle of the left side. The square in A corresponds to the SEM in Fig. 4B, and square in B corresponds to the SEM in Fig. 4C. B. SEM of the frontal surface of the anterior region of the left ctenidium. The rounded ventral tips of the filaments and a low fold of epithelium (thin arrow) form the dorsal and ventral margins, respectively, of the densely ciliated marginal food groove. Thick arrow indicates the non-ciliated median frontal area of one filament. Scale bar = 50 μm. C. SEM of a small section of two filaments seen in B, showing different types of cilia. Thick arrow indicates the non-ciliated median frontal area. Scale bar = 10 μm. Abbreviations: arc, anterior region of the ctenidium; dlp, dorsal labial palp; eu, eulaterofrontal cilia; f, foot; fr, frontal cilia; irc, intermediary region of the ctenidium; mg, marginal food groove; pam, posterior adductor muscle; pr, prolaterofrontal cilia; vlp, ventral labial palp; vm, visceral mass.

ciliated semi-lunar area occurs at each side of the cylindrical region, posterior to the pedal groove. These areas have the same type of cilia as found in the discoid region (Figs. 3A, B) and are separated from each other mid-dorsally and mid-ventrally by areas having sparse flame-like tufts of thin, long cilia (~30 μm long) and flame-like tufts of short cilia (~2 μm long) (Fig. 3D). A similar pattern of flame-like tufts of cilia is also present on the epithelium covering the visceral mass within the limits of the shell valves.

Lips and Labial Palps

The dorsal and ventral lips (Fig. 4A) are slender, shallow, and densely ciliated epithelial folds, with cilia about 5 µm-long and uniform diameter. The ventral labial palps are small ridges of epithelium near the anterior portion of the ctenidia, barely distinguishable anatomically from the ventral lips. In contrast, the dorsal labial palps gradually enlarge posteriorly to form expanded triangular flaps that overhang the ventral palps.

The external and internal surfaces of both palps are smooth. The external surface has dispersed flame-like tufts of cilia previously described for the epithelium of the visceral mass, while the internal surface is densely ciliated, with the same type of cilia as those found on the lips.

Ctenidia

Psiloteredo healdi has only one highly modified homorhabdic eulamellibranchiate demibranch on each side of the body. Each demibranch (ctenidium) has three distinct regions. The anterior and posterior regions are made up of filaments and a marginal food groove; the intermediate region consists only of the food groove (Fig. 1). Careful dissections revealed the efferent and the afferent vessels running along the outer and inner edges of each demibranch, respectively.

The anterior region of the ctenidium, situated immediately posterior to the labial palps, is very short (about 2% of the body length) and is made up of only 15 to 19 filaments (Fig. 4). These filaments are fixed throughout their entire abfrontal surfaces to the epithelium of the visceral mass and their ventral extremities form the dorsal margin of the food groove at the anterior region of the ctenidium. The ventral margin of this groove consists of a low fold of epithelium (Fig. 4B). The frontal surface of each filament of the anterior region of the ctenidium has two longitudinal marginal rows of 10 µm-long frontal cilia, isolated by a non-ciliated mid-frontal area (Figs 4B, 4C, 5A). The two marginal frontal rows of cilia join together at, and completely cover, a short extension of the free distal end of each filament.

A single line of 17 µm-long eulaterofrontal cilia lies along and adjacent to each longitudinal row of frontal cilia (Figs 4C, 5). Prolaterofrontal cilia, revealed only by SEM and reported here for the first time in Teredinidae, occur in a single line inserted between the frontal and eulaterofrontal rows of cilia (Figs 4C, 5A). A longitudinal row of 20 µm-long lateral cilia occurs on both sides of each ctenidial filament. The anterior and posterior filaments of the anterior region of the ctenidia are considered hemifilaments because their morphology and ciliation correspond to the longitudinal half of a normal filament.

The posterior region of the ctenidium is very long (about 68% of the body length) in well-relaxed specimens and has both descending and ascending lamellae (Figs. 2, 6). Specimens frequently stressed by their removal from the wood drastically reduced their posterior regions of the ctenidia to 50% or less of its normal length. It is very difficult to fix

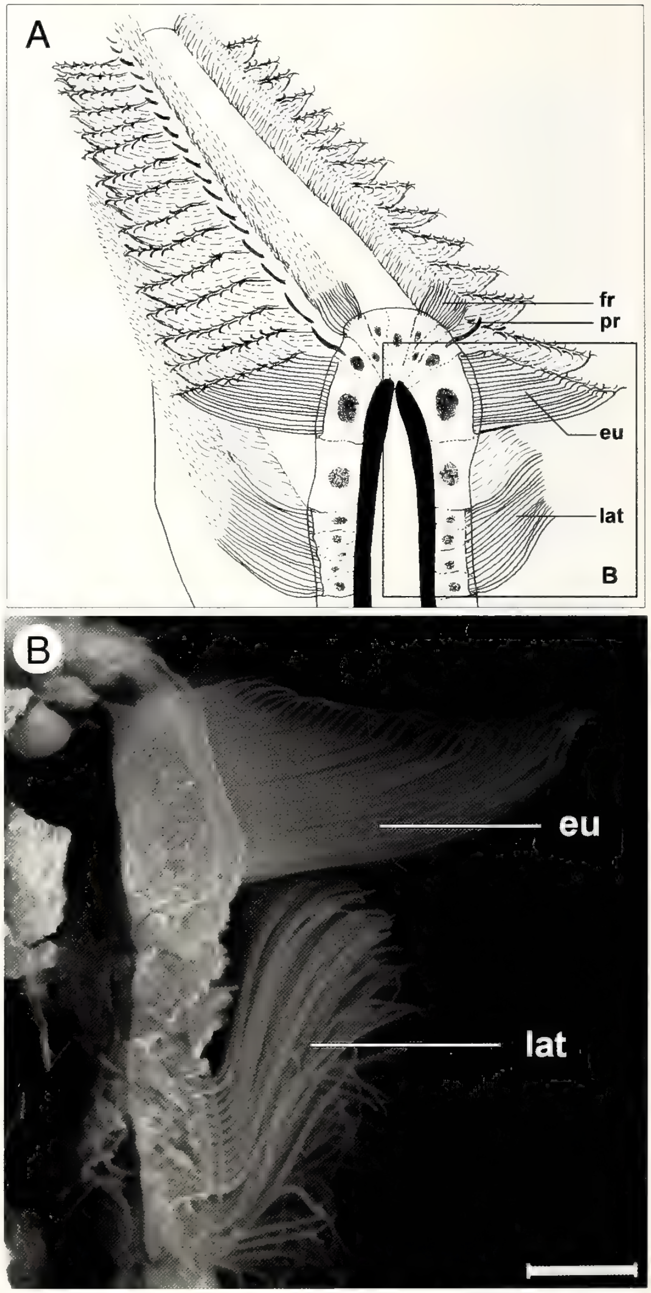

Figure 5. A. Diagrammatic representation of the distal half of a ctenidial filament of *Psiloteredo healdi* to show the types and distribution of cilia. The square corresponds to the SEM in Fig. 5B. B. SEM of a transverse section through the distal half of a filament. Scale bar: 5µm. Abbreviations: eu, eulaterofrontal cilia; fr, frontal cilia; lat, lateral cilia; pr, prolaterofrontal cilia.

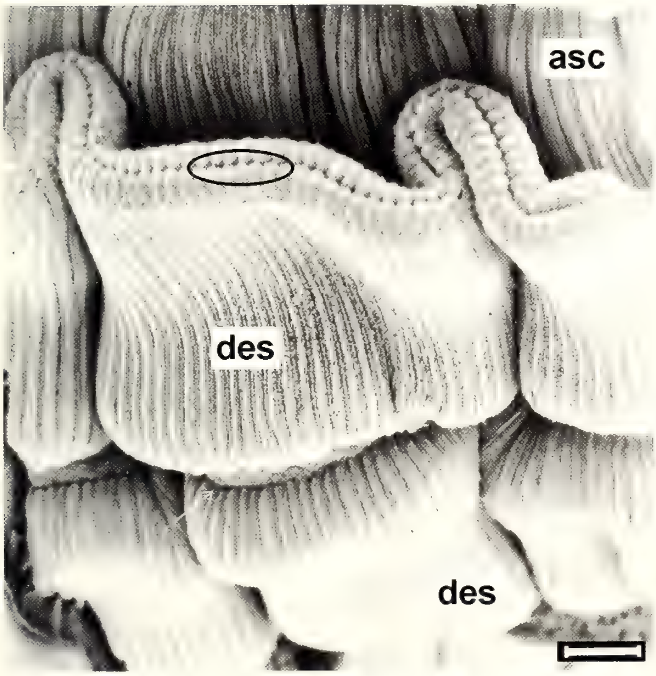

Figure 6. SEM of a well-contracted segment of the posterior region of the ctenidia of *Psiloteredo healdi*. Abbreviations: des, descending lamellae strongly deflected to the sides, exposing the fused ctenidial axes and one marginal food groove (encircled); asc, supra-axial extension of the ascending lamella. Scale bar = 200 µm.

well-relaxed specimens, so the ratio of the length of the posterior region of the ctenidia to the body length is highly variable, but does not exceed 0.7 in well-relaxed specimens.

The height of the posterior region decreases abruptly at its anterior end and gradually at its posterior end. The ascending lamella expands dorsally above the limit of the ctenidial axis, becoming higher than the descending one (Fig. 6).

Joined by their respective ctenidial axes, the right and left ctenidia extend forward from the bases of the siphons until they meet the posterior limit of the visceral mass. From this point the ctenidia and respective axes separate laterally and extend individually, surrounding the visceral mass (Figs. 1-2).

Especially in fixed specimens, the posterior region of each ctenidium remains strongly deflected to the side, completely exposing the internal lamella and the ctenidial axis (Fig. 6). In such condition, the external lamella is bent at a right or acute angle at the level of the ctenidial axis and its dorsal extension has the appearance of a vestigial demibranch. The food groove along the free edge of the posterior region of each ctenidium is deep and densely ciliated. The features and distribution of the cilia of this posterior region of the ctenidium are the same as those described for the anterior region of this organ.

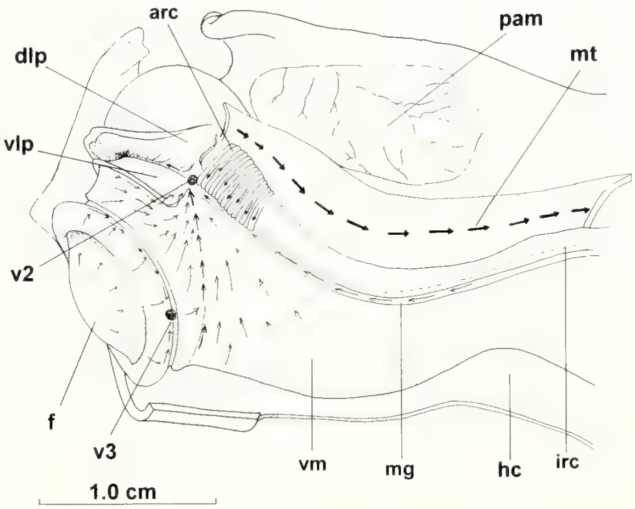

Figure 7. Diagram of the left anterior region of *Psiloteredo healdi*, after removal of the shell. Mantle longitudinally sectioned and respective dorsal half deflected dorsally to show the strong rejection tract on the internal mantle surface (thick arrows). Thin arrows show sorting mechanisms of processing wood particles on the foot, and of processing suspended particles on the anterior and intermediate regions of the left ctenidium. Abbreviations: •, vortex where particles converge. arc, anterior region of the ctenidium; dlp, dorsal labial palp deflected dorsally; f, foot; hc, hypobranchial cavity; irc, intermediate region of the ctenidium; mg, marginal groove; mt, longitudinal mantle rejection tract; pam, posterior adductor muscle; v2, vortex between labial palps and anterior region of the ctenidium; v3, vortex at the periphery of the discoid region of the foot; vlp, ventral labial palp; vm, visceral mass.

The intermediate regions of the ctenidia (Figs 1, 4A-B), comprising only the food groove (~25 µm depth), has smooth, densely ciliated lateral walls.

Ciliary Currents

The main bulk of the visceral mass greatly restricts the anterior portion of the pallial cavity, and practically segregates the routes of two food sources entering from opposite directions: suspended material and wood particles.

The posterior regions of the ctenidia handle plankton and other suspended material brought in by the incurrent flow of water, while the foot, located at the anterior end of the body, deals primarily with extremely fine wood particles drilled by the shell when the animal is excavating.

Route of suspended material (Plankton)

The incurrent flow of water caused by the strong beating of the lateral cilia draws suspended particles and plankton into the mantle cavity, where they are filtered through and size-selected on the elongated posterior regions of the ctenidia.

Frontal currents on both external and internal lamellae carry suspended material onto the free distal edges of the ctenidia (Fig. 2). Here, minute particles of similar size to those of carmine and colloidal graphite are trapped by frontal cilia adjacent to the eulaterofrontal ones and deflected into the food groove. Cilia in this groove carry particles entangled in a fine mucous string toward the mouth. Frontal cilia at the free tip of the filaments retain dense, large particles similar in size to carborundun, as well as clumps or excess fine particles, conducting them anteriorly outside the food groove. Particles traveling on this unprotected, external mouthward current are frequently rejected as they drop to the mantle epithelium. They are often captured directly by the cilia that form the two longitudinal ciliated tracts of the mantle (Fig. 2). These are rejection tracts because they conduct material to and concentrate it in a vortex (v4, Fig. 2A) at the base of the incurrent siphon to be eliminated as pseudofeces.

Intrinsic musculature of the posterior region of each ctenidium permits it to bend, bringing its food groove close to or far from the longitudinal ciliated rejection tract of the mantle. These rejection tracts lie strategically parallel and slightly ventral to the marginal food groove throughout its length. When the food groove and rejection tract are close to one another, the powerful ciliary currents on the latter directly capture unprotected, unwanted material traveling mouthward outside the food groove.

Whenever there is too much food to be processed at a given time the rejection tract may also capture strings of mucus traveling inside the food groove. The voluminous strings flow out the groove. When the food groove and rejection tract are far apart, unprotected particles carried outside the food groove as well as excess particles traveling inside it may reach the anterior extremity of the posterior portion of the ctenidium. However, this material is trapped and accumulated in a vortex (v1, Fig. 2A). At this vortex, the mucous mass gradually grows in size and is finally captured and carried to the base of the incurrent siphon via the longitudinal rejection tracts of the mantle.

Whenever the animal deals with a large amount of suspended matter, the excess of fine particles may be sorted on the ctenidial filaments and carried mouthward. Voluminous strings of mucus with entangled particles traveling within the food groove may surmount the barrier imposed by the v1 vortex and reach the intermediate region of the ctenidia. To prevent a voluminous mass or excess material from reaching and clogging the mouth, the bivalve moves the walls of the intermediate region apart. This allows particles and mucus to be captured by the rejection tracts of the mantle.

Suspended particles that eventually reach and settle on the anterior region of the ctenidia are also carried ventrally and transferred to the marginal food groove. Material arriving at the anterior-most portion of this groove is transported mouthward. When in excess, it is trapped in a second vortex (v2, Fig. 7) lying at the confluence of the labial palps with the first filament of the ctenidium. As in the v1 vortex, when the volume of the mucous mass and entangled particles grows larger it can be caught and eliminated by the rejection tract of the mantle. The free distal end of the dorsal labial palp can also push the mucous mass onto the rejection tract of the mantle.

Route of wood particles

Suction movements caused during excavation of the gallery and ciliary activity on the foot and on the mantle margin around the pedal opening draw wood particles into the anterior portion of the mantle cavity. The discoid region of the foot frequently changes its proportions and shape. Expanding to the sides, the discoid region forms two winged projections that reduce the pedal opening. Concomitantly expanding the mantle edge can completely close the pedal opening. Thus, the mantle edge and foot regulate the inflow of water caused by cilia on the free edge of the mantle as well as the entrance of wood particles into the anterior region of the mantle cavity.

The epithelium of the discoid region of the foot has intense centrifugal ciliary activity, transporting particles to the periphery of the organ (Fig. 7). When viewed with light microscopy, both the cilia and their respective currents appear continuous throughout the discoid region of the foot. However, SEM images revealed alternate ciliated and non-ciliated rings. This suggests that muscular activity in the foot may also play a critical role in the dynamic flow of particles.

Reduction of the diameter of the discoid region brings the ciliated ring-shaped areas together, enabling the rapid transfer of wood particles from one to another, as if the discoid region of the foot was a uniformly and densely ciliated surface. Particles reaching the dorsal quadrants of the peripheral ciliated ridge of the discoid region are conducted ventrally, converging onto two vortices (v3, Fig. 7) lying at the midpoint along the margin of the two ventral quadrants. Particles reaching the periphery of each ventral quadrant also converge to these v3 vortices. Material accumulated in these v3 vortices is immediately transferred to the ciliated semi-lunar areas on each side of the cylindrical region of the foot. When analyzed with light microscopy, such peripheral currents and respective vortices may erroneously be interpreted as occurring within the deep ring-shaped groove, which separates the discoid from the cylindrical regions of the foot. SEM images showed that this groove lacks cilia. Muscular activity brings together the outer edge of the peripheral ciliated ridge of the discoid region and the semi-lunar ciliated areas on the cylindrical region of the foot, concealing the deep, non-ciliated groove between them. Wood particles traveling ventrally on the periphery of the discoid region, or concentrated in its ventrolateral v3 vortices, may now be caught by cilia of the semi-lunar areas and transferred dorsally to the palps and oral groove. With relaxation of the musculature of the foot, and consequent expansion of the non-ciliated groove, the latter may act as a barrier interrupting the direct transfer of wood particles to the cylindrical region of the foot.

Ciliary activity on the semi-lunar areas of the cylindrical region of the foot, as well as on the adjacent areas, conducts wood particles toward the point of confluence of the labial palps with the anterior extremities of the ctenidia (v 2, Fig. 7). Cilia along the posterior edges of the semi-lunar areas create strong dorsal currents that conduct the bulk of material to the v2 vortices. Material concentrated in these vortices can be accepted and conducted mouthward along the oral groove, or rejected when the mucous mass is large enough to be caught and pulled by cilia along the vigorous longitudinal rejection tract of the mantle.

Isolated particles not trapped and selected both in the wood (anterior) and suspended material (posterior) routes may settle on the lips and labial palps.

Ciliary activity on the external and internal epithelia of the dorsal labial palps concentrates particles at the free distal ends of these organs. Bending toward the mantle, the dorsal labial palps allow particles to be captured and eliminated via the longitudinal rejection tracts of the mantle. Alternatively, the material may be ingested by contacting the marginal food-groove. Weak currents conducting particles to the v2 vortices (Fig. 7) were detected along the ventral surface of the ventral lip and on the inconspicuous ventral labial palps.

Posterior to the shell valves, weak ciliary currents on the epithelium lining the visceral mass catch isolated particles entering via both anterior (wood) and posterior (suspension) routes and convey them ventrally. Cilia of the mantle epithelium close to this portion of the visceral mass capture and reject such material.

Cleansing currents on the internal mantle epithelium capture and remove unwanted and excess wood and suspended material, carrying them onto and concentrating them in a v4 vortex (Fig. 2) at the base of the incurrent siphon to be discarded as pseudofeces.

DISCUSSION

Psiloteredo healdi is unique in possessing longitudinal rejection tracts of the mantle fusing together near the base of the incurrent siphon and extending slightly into this organ, as well as a vortex (v4, Fig. 2) in this region. In *Teredo norvegica* Shumacher, 1817 (= *Noteredo norvagica* [Spengler, 1792]) and *Teredo megotara* Hanley, 1848 (= *Psiloteredo megotara* [Hanley, 1848]) studied by Purchon (1941) and in *Teredo furcifera* von Martens, 1894, and *Teredora princesae* (Sivickis, 1928) as described by Saraswathy and Nair (1971), these tracts are fused in extension as long as the posterior regions of the ctenidia. In *Bankia fimbriatula* Moll and Roch, 1931 studied by Martins-Silva (1997) rejection tracts are joined at the base of the incurrent siphon with no posterior extension. In *Xylotrya gouldi* Bartsch, 1908 (= *Bankia gouldi* [Bartsch, 1908]) analyzed by Sigerfoos (1908), *Nausitora hedleyi* Schepman, 1919, studied by Saraswathy and Nair (1971), and *Nausitora fusticula* (Jeffreys, 1860) studied by Lopes and Narchi (1998), these tracts are separated throughout their lengths. Visualized only by SEM, the fusion and respective extension of the rejection tracts in *P. healdi* seem to be related to and responsible for the presence of a v4 vortex (v4, Fig. 2), where rejected material agglomerates before being eliminated as pseudofeces. Additional experiments will be required to understand whether these different configurations of tracts in different species could be related to the efficiency of the cleansing mechanisms of the mantle cavity.

By comparing the positions of the afferent and efferent blood vessels in the single demibranch of teredinids with those of bivalves having two demibranchs, Purchon (1941) concluded that in Teredinidae the single demibranch is the external one. However, Ridewood (1903), Sigerfoos (1908), Atkins (1937), and Turner (1966) disagreed. Our examination of the positions of the vessels in *Psiloteredo healdi* indicates that it is the external demibranch, supporting Purchon (1941).

SEM allowed precise identification of the types and distribution of cilia of the ctenidial filaments of *Psiloteredo healdi*. The ctenidial morphology, types of cilia, and their distribution in this species are similar to those described in *Xylotrya gouldi* by Sigerfoos (1908). However, the prolaterofrontal cilia described here in *P. healdi* have not been described previously in any teredinid and their precise function in bivalves is not known. Their location parallel to the eulaterofrontal cilia may increase the efficiency of filtering water and prevent excess and large particles from entering the marginal food groove. The presence of two rows of frontal cilia separated by a median, non-ciliated longitudinal area here described for *P. healdi* have only been described for *X. gouldi* (Sigerfoos 1908) and for *Bankia fimbriatula* (Martins-Silva 1997).

Turner (1966) believed the reduction of the ctenidium in teredinids to only one demibranch, as well as its reduction in extent and height, reflected the reduced importance of plankton and suspended material as food, as wood is an important supplemental source for these animals. She considered the ctenidia of *Psiloteredo healdi* as reduced compared with other species, especially with those of *Teredora* spp. in which the ctenidia are not divided into three regions but have a continuous row of filaments from the labial palps to the bases of the siphons. In the context of the teredinids, which have highly modified ctenidia, the posterior regions of the ctenidia of *P. healdi* cannot be considered reduced and of lesser importance in food capture. The posterior regions of the ctenidia extend for about 68% of the body length of the bivalve, they have specialized deep food grooves and tall lamellae, and the external lamellae expand dorsally. The ratio of 0.7 for the length of the posterior region of the ctenidia to the total body length of *P. healdi* measured here differs from the ratio of 0.4 obtained by Turner (1966). This discrepancy may be attributed to the small number of specimens (only three preserved animals) and the lack of relaxation in the animals analyzed by Turner (1966).

The weak sorting devices on the ctenidia of *Psiloteredo healdi*, restricted to the free distal ends of the filaments, are compensated for by the strategic positions of the longitudinal rejection tracts of the mantle, which capture excess material conducted mouthward outside and within the marginal food groove. The ability of the posterior regions of the ctenidia to make contact with the rejection tracts of the mantle most likely enhances the efficiency of these cleansing mechanisms in the corresponding mantle cavity portion. Lopes and Narchi (1998) observed the same behavior in *Nausitora fusticula*.

The reduced foot, with a discoid region separated from the cylindrical one by a deep ring-shaped groove, is characteristic of Teredinidae. According to Miller (1924), reduction of the foot and changes in its musculature constitute an important adaptation to the drilling habit. The ciliary currents lining the pedal epithelium remove wood particles into the mantle cavity, preventing them from accumulating and blocking the blind end of the tunnel and obstructing the foot and shell functioning. The specialization of the cilia also allows these wood-boring bivalves to select the finest fragments of wood for ingestion and to remove unwanted or excess material to the rejection routes on the mantle epithelium.

The presence of cilia and ciliary currents on the feet of teredinids have been described and illustrated by Sigerfoos (1908), Purchon (1941), Morton (1970), Saraswathy and Nair (1971), Martins-Silva (1997), and Lopes and Narchi (1998). None of these authors, however, provide details about the types and distribution of the cilia on the pedal surface. Only SEM images revealed such characteristics in *Psiloteredo healdi*, and allowed us to understand their functioning.

The distribution of cilia into rings separated by non-ciliated areas at the discoid region of the foot and in semi-lunar areas segregated by zones with scattered flame-like tufts of cilia in the cylindrical region show the complexity of the pedal epithelium in *Psiloteredo healdi*. SEM images allowed us a more accurate understanding of specialization of cilia in this organ. The foot serves not only as an accessory attaching tool, assisting the shell with its drilling action, but is also crucial in wood processing.

Only the non-ciliated central area of the discoid region probably acts as a sucker, attaching the foot to the blind end of the tunnel when the animal is actively drilling wood with the shell. By retracting and expanding the foot and bringing the ciliated areas in the discoid region together and apart, the animal controls the number of wood particles and the velocities of the fluxes into the anterior portion of the mantle cavity and onto the ciliated areas on the cylindrical region of the organ.

Contrary to what Lopes and Narchi (1998) found in *Nausitora fusticula*, the foot groove of *Psiloteredo healdi* has no cilia. This strongly suggests that it may act as a barrier for avoiding or reducing transport of wood particles from the discoid to the cylindrical region of the foot. By retracting the foot the bivalve may close the deep, non-ciliated ring-shaped groove, bringing in contact the peripheral ciliated ridge at the discoid region with the ciliated areas on the cylindrical region of the foot. This likely improves the influx of particles into the mantle cavity, the bulk of which may be submitted to the sorting devices before rejection. By changing its proportions and shape, the discoid region may form wing-shaped lateral projections that, coordinated with the expanding mantle edges, interfere with the influx of water and wood into the anterior portion of the mantle cavity. Expanding the ring-shaped groove favors rejection, as particles may be caught directly by cleansing or rejection currents on the adjacent mantle epithelium instead of being submitted to the sorting devices on the cylindrical portion of the foot. Such mechanisms of control of the pedal opening by the foot and free mantle edges are not unique to *P. healdi*; they have also been described in *N. fusticula* (Lopes and Narchi 1998). They may be universal among the teredinids.

The labial palps of *Psiloteredo healdi* are similar to those of *Teredo fatalis* Quatrefages, 1849 (= *Neoteredo norvagica* [Spengler, 1792]) studied by Quatrefages (1849); *Xylotrya gouldi* and *Teredo navalis* Linnaeus, 1758 studied by Sigerfoos (1908); *T. navalis* studied by Lazier (1924) and Martinez (1987); *Nausitora hedleyi*, *Teredo furcifera*, and *Teredora princesae* studied by Saraswathy and Nair (1971); and *Teredo petiti* Récluz, 1849 (= *Psiloteredo senegalensis* [Blainville, 1828]) and *Teredo adami* Moll, 1941, (= *Neoteredo reynei* [Bartsch, 1920]) studied by Rancurel (1971). The palps of these species are intermediate in size compared with the small palps described by Lopes and Narchi (1998) in *Nausitora fusticula* and the very large ones described by (Purchon, 1941) in *Teredo norvegica*. According to Purchon (1941), the palps of *T. norvegica* have folded inner surfaces capable of qualitative selection, similar to those of bivalves that burrow into unconsolidated substrates.

The absence of folds and the presence of only one type of cilium on the inner surfaces of the palps suggest little selection by these organs in *Psiloteredo healdi*. Before reaching the palps, suspended particles and plankton entering through the incurrent siphon (route of suspended material) have been sorted by the ctenidia. Unwanted or excess material is prevented from reaching the mouth both by the action of the vortices along the marginal food grooves (v1, Fig. 2 and v2, Fig. 7) and the strong rejection tracts of the mantle. Sorting devices on the foot, combined with the v2 vortex action and the rejection tracts of the mantle also prevent unwanted and excess wood particles entering through the pedal aperture (route of wood particles) from reaching the mouth. Instead of having a selective function, the palps in *P. healdi* work like gates, preventing excess material coming from both "wood" and "suspension" routes and trapped on the v2 vortices from reaching the oral groove, and mouth.

Turner (1966) and Saraswathy and Nair (1971) considered that an evolutionary trend toward reduction of palp function in Teredinidae has occurred with the change to a predominantly wood diet. The presence of moderately developed dorsal labial palps, and particularly of long posterior portions of the ctenidia, strongly suggest that plankton and others suspended particles are important food items for *Psiloteredo healdi*. The efficient sorting mechanisms on the ctenidia and foot, in conjunction with the cleansing mechanisms on the mantle epithelium, compensate for the reduction of the palps.

Lopes *et al.* (2000) found that the diameter (relative to body size) of the appendix (= stomach caecum) of *Psiloteredo healdi* increases with age. When the animals are small they feed primarily on suspended particles and plankton. The authors propose that a wider appendix allows a more efficient digestion of wood. Hoagland and Turner (1981) hypothesized that flexibility in food source in Teredinidae can be related to crowding and that active drilling may cease in favor of filter feeding. Sorting mechanisms on the organs and structures of the mantle cavity in *P. healdi* are specialized to handle these two discrete food sources independent of age. Additional experiments are required to test if crowding or other environmental factors induce these animals to switch between alternative feeding habits.

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Continuity of flow through the gastropod mantle cavity

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Abstract: Gastropod mantle cavities play a central role in theories of gastropod evolution. I used anatomical dimensions and flow velocities to test whether the flow of water through a gastropod mantle cavity follows the same Principle of Continuity that describes flow through pipes. Measurements of the dimensions of the paths through which water flows in the marine gastropods *Diodora aspera* (Rathke, 1833) and *Fasciolaria hunteria* (G. Perry, 1811) illustrate that, as expected, the largest total cross-sectional area is located at the many parallel channels between gill lamellae and that the smallest cross-sectional areas lie at the incurrent and excurrent windows, where the water enters and exits the shell. Measurements of flow rates at the incurrent and excurrent windows indicate that flow through the mantle cavities in these animals follows the Principle of Continuity. This, in turn, permits the prediction of flow rates along the length of the path of flow.

Key words: *Diodora*, *Fasciolaria*, biomechanics, ctenidia, gills

The anatomy of "prosobranch" gastropods is surprising and puzzling. An anterior mantle cavity houses the respiratory organs (gills, usually called ctenidia) as well as the openings of the ducts for eliminating urine, feces, and gametes. The dorsal internal surface of the mantle cavity contains a hypobranchial gland, which lies over the gill and secretes mucus. In general, water flow through this cavity is asymmetric, entering at the anterior or left, passing over the gill or gills, and exiting to the posterior or right (Voltzow 1994).

In what is generally assumed to be the primitive condition, vetigastropods of the superfamilies Pleurotomarioidea and Fissurelloidea (the slit shells, abalone, and keyhole limpets) have two gills and a dorsal slit or openings (tremata) in their shells (Fig. 1A, B). The vast majority of marine prosobranchs, however, the trochoideans, neritoideans, and the caenogastropods, show a derived condition in which the mantle cavity is asymmetric (Yonge 1947). The right gill and its related organs have been lost (Fig. 1C, D).

For over 150 years, the mantle cavity (also referred to as the pallial cavity) has played a central role as a source of information for the classification of gastropods (Bieler 1992, Voltzow 1994, Lindberg and Ponder 2001). The evolutionary scenario developed by Yonge (1947) was elaborated by Knight (1952) and figures prominently in Fretter and Graham's (1962, 1994) description of the evolution of gastropod mantle cavities (see Lindberg and Ponder 2001, for an interesting reconstruction of the history of these ideas). Although most versions show the reduction of mantle cavity organs as a single evolutionary event, Yonge's (1947) original paper and recent phylogenetic analyses of gastropods and related molluscs by Ponder and Lindberg (1997) indicate that the reduction in gill number and its related suite of morphological alterations happened at least four times over the course of gastropod evolution (Lindberg and Ponder 2001).

The distribution of characters mapped on current phylogenetic trees are not congruent with many aspects of the traditional evolutionary scenario (Lindberg and Ponder 2001). In fact, the mantle cavity consists of a suite of characters that have not always evolved in consort. For example, paired gills are generally depicted as creating a symmetrical pair of currents that enter the mantle cavity on either side of the head. Although this is the case in fissurellids such as *Diodora aspera* (Rathke, 1833), whose mantle cavity is bilaterally symmetrical, it is not the case for the pleurotomarioideans *Haliotis kamtschatkana* Jonas, 1845 and *Perotrochus maureri* Harasewych and Askew, 1993, whose mantle cavity is not bilaterally symmetrical (Voltzow 1983, personal observation). Before we can understand the evolution of the gastropod mantle cavity, however, we need a better understanding of its functional morphology.

Design elements of the mantle cavity

The respiratory function of the gastropod mantle cavity results from the coordination of a suite of design elements: an incurrent window, an incurrent chamber, the pump, the exchange surface, an excurrent chamber, and an excurrent

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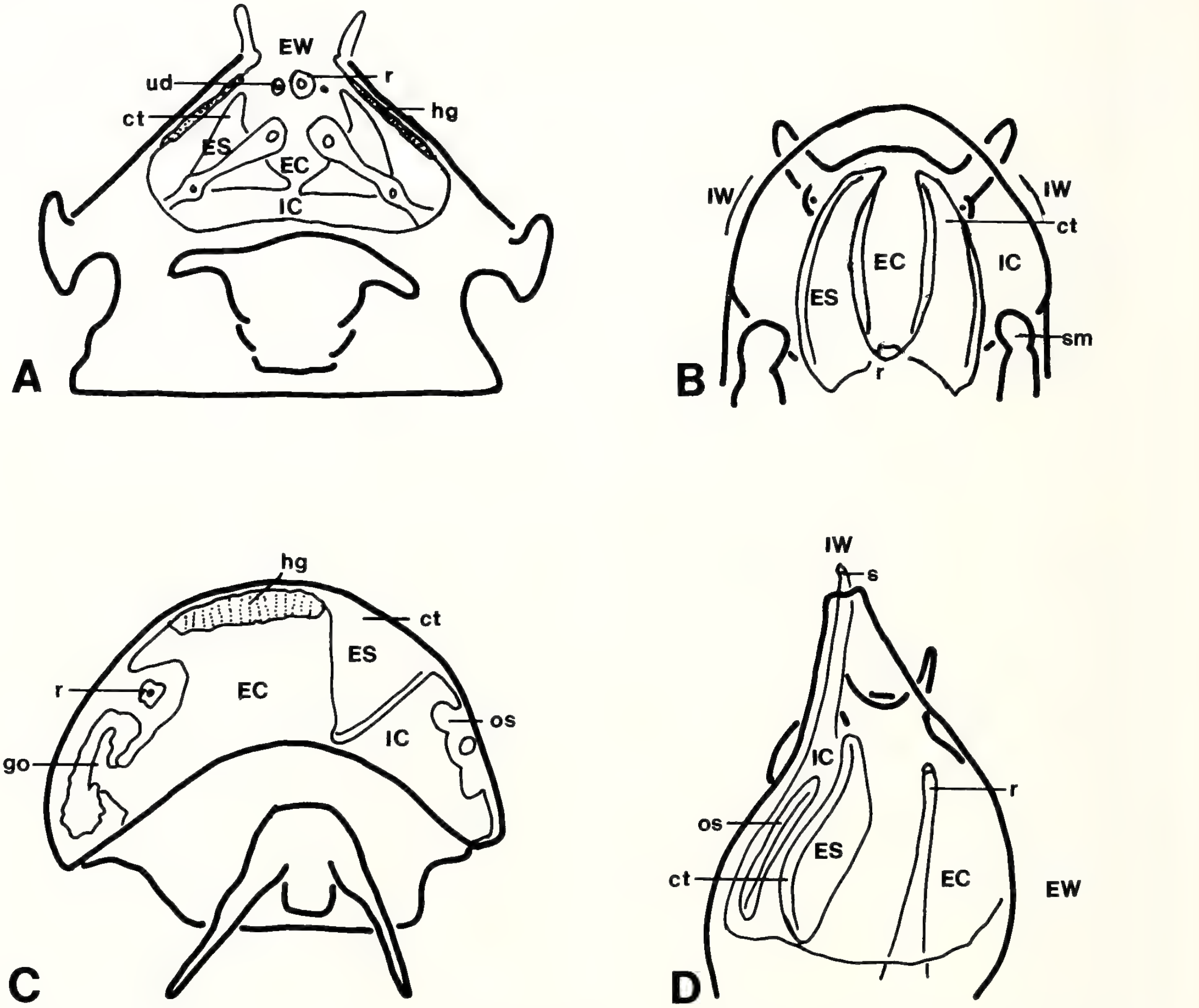

Fig. 1. Diagrams of transverse (A, C) and dorsal (B, D) views of the mantle cavities of *Diodora aspera* (A, B) and *Fasciolaria huneria* (C, D) based on Fretter and Graham (1962, Fig. 48), observations of live animals, and camera lucida drawings of dissections and histological sections. ct = ctenidium, go = gonadal opening, hg = hypobranchial gland, os = osphradium, r = rectum, s = siphon, sm = shell muscle, ud = urogenital duct; EC = excurrent chamber, ES = exchange surface, EW = excurrent window, IC = incurrent chamber, IW = incurrent window

window (Fig. 2). The incurrent and excurrent windows are usually specific regions of the shell and mantle that control the shape and size of the incurrent and excurrent streams. These may include quite subtle or obvious elaborations including siphons, tremata, slits, or other openings of the shell and underlying mantle. The shapes of the incurrent and excurrent chambers are defined by the overlying mantle and shell, the gill or gills, and the surfaces of the animal's head and anterior visceral mass (often called the "floor" of the mantle cavity). Cilia beating on the surface of the gill and sometimes on the interior surface of the mantle and other structures provide the pump. The vascularized gill is the primary exchange surface; gases may be exchanged across other surfaces as well.

Although the general anatomy of many species of gastropods has been described (e.g. Simroth 1896-1907, Fretter and Graham 1962, 1994, Hyman 1967, Voltzow 1994) there are relatively few detailed accounts of all of the design features of the mantle cavity for any given species. In particular, because most morphological studies are performed on retracted, dead animals, they include little information about the locations of the incurrent and excurrent windows or the position of the functioning ctenidium within the mantle cavity. Many of the design elements are only recognizable in living animals because they are characterized by their functions rather than by their structure.

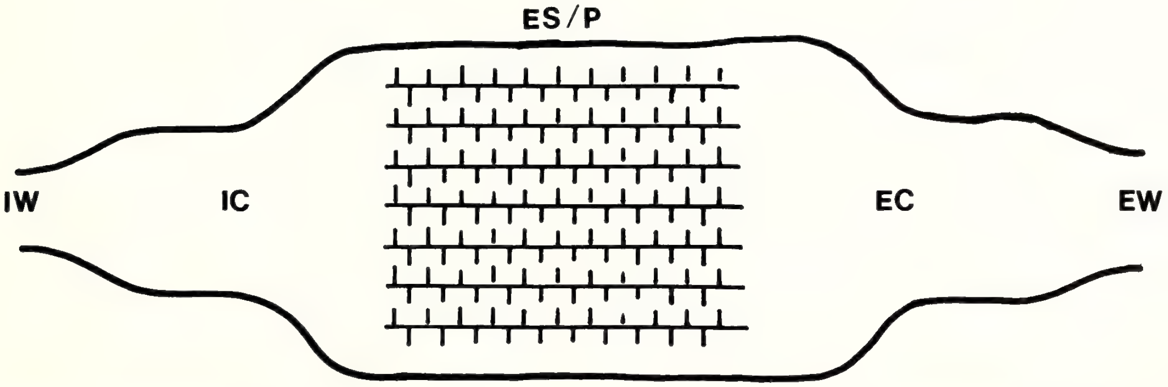

Fig. 2. Diagram of the design elements of the molluscan mantle cavity. EC = excurrent chamber, ES/P = exchange surface/pump, EW = excurrent window, IC = incurrent chamber, IW = incurrent window

The Principle of Continuity

The geometry of the design elements has important implications for function. To understand some of the fundamental elements of mantle cavity design I compared animals of two species, one that has two bipectinate ctenidia and a bilaterally symmetrical mantle cavity, *Diodora aspera*, and one that has a single set of mantle cavity organs and a single, monopectinate ctenidium, *Fasciolaria hunteria* (G. Perry, 1811). I modeled the paths by which the water flows through the mantle cavities of these animals as pipes with parallel branches. The volume flow rate, or the product of the cross-sectional area and velocity, remains constant along the length of a pipe, a feature known as the Principle of Continuity (Vogel 1981). Continuity has been used to explain a number of biological phenomena, including flow through sponges, xylem vessels, and the vertebrate circulatory system (Vogel 1981). To test if flow through the gastropod mantle cavity follows this physical feature of the movement of fluid through a pipe, I measured the cross-sectional areas of the design elements of individuals of both species, calculated what the predicted ratio between incurrent and excurrent velocities would be if the Principle of Continuity were applicable, and compared the predicted ratios to those of measured flow rates. The results demonstrate that the mantle cavities of these gastropods conform to the Principle of Continuity, making it possible to estimate flow velocities at the surface of the ctenidium and at other points within the mantle cavity.

MATERIALS AND METHODS

Individuals of *Diodora aspera* (Rathke, 1833) were collected from Lime Kiln Point and Cattle Point, San Juan Island, Washington, USA. They were maintained in the running seawater system at the Friday Harbor Laboratories of the University of Washington, San Juan Island, Washington, USA, and studied within two months of collecting. Additional individuals were shipped to Scranton, Pennsylvania, USA, and maintained in a 150L aquarium chilled to 10-12°C. Individuals of *Fasciolaria hunteria* (G. Perry, 1811) were obtained from Gulfcoast Specimen Marine Laboratories Inc., Panacea, Florida, USA, and maintained in 38L aquaria in Scranton, Pennsylvania, USA, at room temperature (approximately 20-24°C).

Shell length, shell width, and the wet masses of each animal and shell were measured with a vernier caliper and a Mettler PE 160 electronic balance. Live animals were observed and photographed while in the aquaria and were videotaped while crawling and resting on the sides and bottoms of small tanks constructed from high-quality glass. Anatomical measurements were made from photographs, videotapes, drawings, and dissections of live and freshly relaxed (in 7.5% $MgCl_2 \cdot 6H_20$) animals. These anatomical measurements were used to calculate the cross-sectional area of each design element of the mantle cavity for each species. Over the course of this study, at least 10 individuals of each species were examined. Because of variation among animals, the results section reports measurements from three similarly-sized individuals of each species.

Flow patterns were visualized with fluorescein dye or milk released around animals in still water (Voltzow and Collin 1995). Incurrent and excurrent regions along the shells were identified with dye streams. Flow rates were measured by analyzing videotapes of neutrally buoyant particles in the incurrent and excurrent flowstreams. A glass rod (5 mm diameter) mounted vertically immediately in front of a Uniphase Model 1126 Helium-Neon laser spread the point of light into a plane. Particles (30-40 μm diameter) that occur naturally in seawater were visualized with a 50 mm Nikon SLR macrolens with extension tube mounted on a Panasonic WV-D5000 CCD videocamera. Particles of this size move similarly to water through a molluscan gill (Grünbaum *et al.* 1998). Samples of 25 μm diameter polystyrene microspheres (Polysciences, Inc.) were added for verification of flow velocities. Videotapes were recorded on a Panasonic AG-1980P video cassette recorder and analyzed with NIH Image 1.61 on a Power Macintosh 8500.

To visualize the mantle cavities as series of cylindrical tubes, I calculated what the radius of a cylinder would be to have the equivalent given cross-sectional area of each design element. These radii provided the linear dimensions (diameter of a pipe = 2r) of the horizontal dimensions in Figure 3.

If the Principle of Continuity can be applied to the mantle cavities of these species of gastropods, the volume flow rate (e.g. mm^3/s) should be the same throughout the mantle cavity at any given time. To test this, I calculated what the ratio of the incurrent to excurrent velocities would be based on the measured cross-sectional areas of the incurrent and excurrent windows (Table 1). I then compared the predicted ratios to the ratios of measured incurrent and excurrent velocities. Because I had direct measurements for both windows for individuals of similar sizes in both species, I was able to compare these predicted velocities to actual measurements.

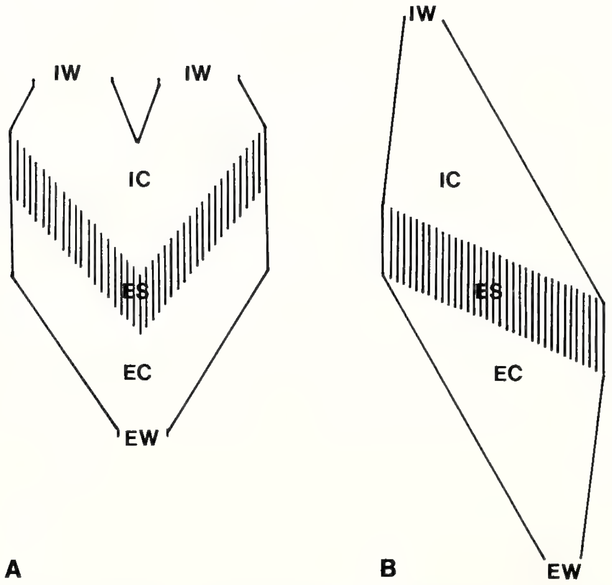

Fig. 3. Diagrams of the mantle cavities of *Diodora aspera* (A) and *Fasciolaria hunteria* (B) modeled as series of parallel pipes. Linear dimensions in these diagrams correspond to the diameters of cylindrical pipes of equivalent cross-sectional areas to the anatomical measurements given in Table 1. EC = excurrent chamber, ES = exchange surface, EW excurrent window, IC = incurrent chamber, IW = incurrent window

Table 1. Anatomical measurements, calculated diameters and radii (r) of pipes, relative velocities, and measured velocities of the principal design elements of the mantle cavities of *Diodora aspera* and *Fasciolaria hunteria.* Values given here are for individuals of *D. aspera* of approximately 14 g total wet mass and individuals of *F. hunteria* of approximately 13 g total wet mass.

	Cross-sectional area (mm^2)	Radius (mm)	Diameter if cylindrical (mm)	r^2 (mm^2)	Predicted relative velocities	Measured velocities (cm/s)	Approximate volume flow (mm^3/s)
Diodora aspera							40
Incurrent window (each of pair)	20	2.5	5.0	6.5 total 12.5	3.10	0.1	
Exchange surface (each of pair)	60	4.4	8.8	19.4 total 38.8	1	0.03*	
Excurrent window	6.6	1.5	3	2.25	17.2	0.6	
Fasciolaria hunteria							30
Incurrent window	4.9	1.24	2.5	1.53	10.5	0.6	
Exchange surface	50	4	8	16	1	0.06*	
Excurrent window	7	1.5	3	2.25	7.1	0.36	

* Velocities at the exchange surfaces were calculated based on the Principle of Continuity.

RESULTS

Design Elements

Each individual of *Diodora aspera* had an incurrent window on either side of its head, just posterior to the cephalic tentacle, where the mantle edge was slightly lifted (Fig. 1B). The size and shape of each incurrent window was quite plastic; an animal could lift the edge of the mantle to control where and how quickly water entered. In an animal whose total (shell and tissue) wet mass was 14.34 g and whose maximum aperture diameter was 46.5 mm, each incurrent window had a cross-sectional area of about 20 mm^2 (Table 1). The only obvious features of the shell that indicated where the water entered were the anterior tips of the muscle scars. The incurrent chambers consisted of the outer, ventral portions of the mantle cavity distal to the pair of ctenidia (Fig. 1A, B). They varied in length from the short distance between the mantle to the anterior of the gill to the much longer distance between the mantle and the posterior end of the gill, or from 3 to 10 mm in a 14 g animal. The pump consisted of the cilia on the gill; the principal exchange surface consisted of the series of bipectinate lamellae of the two ctenidia. The gill of a relaxed 14 g animal, for example, was about 17 mm long; each lamella had a height of about 3.5 mm. In life, the gills were extremely inflated, so the exchange surface was quite large. The excurrent chamber consisted of the dorsal, proximal portion of the mantle cavity (Fig. 1A, B). Its length varied along the length of the ctenidium; long at the anterior of the gill, short at the posterior of the gill. The excurrent window was delimited by the mantle tissue lining the apical opening of the shell. It was ultimately restricted in diameter by the shell, but was also controlled by the mantle, which formed a short siphon that extended beyond the shell surface.

In *Fasciolaria hunteria*, the incurrent window was formed by the siphon (Fig. 1D). Because the siphon is a rolled sheet of tissue and not a fused tube, the shape and size of the incurrent window could be quite plastic, varying greatly in diameter and length from a small, round opening at the tip of the siphon of the shell (4.9 mm^2 in cross-section in an animal whose total wet mass was 12.56 g and whose shell length was 46.0 mm) to a broad (approximately 16 mm) slit. The effect of this was to greatly decrease or increase the size of the incurrent window and thus greatly increase or decrease, respectively, the velocity of the incurrent stream. The incurrent chamber consisted of the region between the incurrent window and the gill (Fig. 1C, D). It varied from being a quite short distance at the anterior of the gill to quite a long distance (the length of the gill) at the posterior. The incurrent chamber was occupied by the osphradium, although some ctenidial leaflets extended anteriorly and posteriorly beyond the length of the osphradium. Although the cilia on the ctenidium served as the pump, their action was probably enhanced by the cilia on the large osphradium. The exchange surface consisted primarily of a single monopectinate ctenidium. The ctenidium of a relaxed 13 g animal measured about 25 mm long, 2 mm high, and 5.5 mm wide. The excurrent chamber consisted of the region between the ctenidium and the excurrent window (Fig. 1C, D). Once again, the distance varied along the length of the ctenidium; long at the anterior of the gill, short at the posterior of the gill. The excurrent window consisted of the portion of the aperture located at the posterior end of the excurrent channel or groove of the shell and measured about 7 mm^2 in a 13 g animal.

Modeling the mantle cavities of these species as a series of parallel pipes accentuated the basic architectural differences (Fig. 3). The pair of incurrent openings and large, paired ctenidia of *Diodora aspera* create a bilaterally symmetrical mantle cavity divided into incurrent and excurrent regions by diagonally oriented ctenidia. The excurrent chambers fuse and water exits through a restricted excurrent window. In contrast, the elongate siphon of *Diodora aspera*, its asymmetrically placed single ctenidium, and spiral shell result in an elongated mantle cavity restricted at both the incurrent and excurrent windows.

Applicability of the Principle of Continuity

Table 1 presents the corresponding flow rates at the various design elements within the mantle cavity. For an individual of *Diodora aspera* of 14 g total wet mass, the flow at the excurrent window was approximately 0.6 cm/s (Table 1), yielding a volume flow of approximately 40 mm^3/s. For an individual of *Fasciolaria hunteria* of 13 g total wet mass, the flow at the incurrent window was approximately 0.6 cm/s, yielding a minimum volume flow of 29.4 mm^3/s. If the Principle of Continuity can be applied to the mantle cavity of *Diodora aspera*, then, setting the flow at the gill equal to 1 (arbitrary units), based on anatomical measurements the relative velocities at the incurrent and excurrent windows should be 3.10 and 17.2, respectively, giving a ratio of incurrent to excurrent velocities of 0.18. Measured incurrent and excurrent velocities in similarly sized animals were 0.1 cm/s and 0.6 cm/s, respectively, or a ratio of 0. 17. Similarly, if flow at the gill equals 1 (arbitrary units), then the predicted relative velocities of water flow at the incurrent and excurrent windows of *Fasciolaria hunteria* should be 10.5 and 7.1, respectively. The measured incurrent and excurrent velocities of similarly-sized individuals were 0.6 cm/s and 0.36 cm/s. The predicted ratio of incurrent to excurrent flows was 1.5 and the ratio of measured flows was 1.7.

DISCUSSION

The two species studied present some interesting contrasts and similarities. *Diodora aspera* possesses the presumed primitive condition of paired bipectinate ctenidia and associated organs. Because of the pressure difference due to the difference in height between the incurrent and excurrent windows, they are capable of using an induced flow to direct water through the mantle cavity (Murdock and Vogel 1978, Voltzow and Collin 1995). The incurrent window is relatively more plastic compared to the excurrent window, which is restricted by the shell. *Fasciolaria hunteria*, on the other hand, represents the derived condition of a single monopectinate ctenidium. Because the incurrent and excurrent windows are approximately the same height from the substrate (in fact, the incurrent window is often elevated above the substrate), an induced flow is not possible. The excurrent window is relatively small and only somewhat plastic in these animals, but the incurrent opening can vary greatly from a small circle to an elongate slit.

Individuals of *Diodora aspera* are capable of creating a negative pressure at the excurrent window; water was occasionally pulled into the mantle cavity at the apical opening. This flow reversal was always accompanied by an increase in area of the excurrent window. Thus, the phenomenon appeared to be resulting from a decrease in pressure due to an increase in volume, rather than due to a reverse of ciliary movement. Similarly, individuals of *Fasciolaria hunteria* occasionally appeared to "blow" out their incurrent windows. Again, this appeared to be due to muscular contractions when the animal was irritated by dye released at the tip of the siphon.

Because of the similarity between the measured and predicted ratios of the incurrent to excurrent velocities in these species, I conclude that the Principle of Continuity can be applied to understand the dynamics of flow through gastropod mantle cavities. This permits some predictions. In both species, the largest cross-sectional area, and thus the slowest flow rates, should occur at the gill surface. Just as the geometry of the capillary beds of vertebrates causes them to have the slowest flow rate (Vogel 1981), so the many parallel passages between the lamellae of the ctenidia present the largest cross-sectional area and therefore should cause the greatest reduction in flow rate. In animals of sizes similar to those of this study, therefore, water should move approximately 0.03 cm/s at the gill surface in *Diodora aspera* and approximately 0.06 cm/s in *Fasciolaria hunteria*.

The smallest cross-sectional area, and therefore the highest velocity, occurred at the excurrent window in *Diodora aspera* but at the incurrent window in *Fasciolaria hunteria*. In both species, the diameter of the design element that was the site of the highest velocity was constrained by the shell and its soft tissue lining. By controlling the mantle lining the excurrent and incurrent openings, an animal can control the velocity of water through the entire mantle cavity.

In gastropods having the primitive condition of two bipectinate ctenidia, such as *Diodora aspera*, flow through paired incurrent windows can be controlled primarily by manipulations of the soft tissue, or mantle epithelium. In contrast, the excurrent window was extremely restricted by a narrow opening in the shell. By controlling the mantle lining these openings, an animal can control the rate of movement of water through the entire mantle cavity. Gastropods such as *Fasciolaria hunteria* that have the derived condition of one monopectinate ctenidium appear to have reversed the site of minimal cross-sectional area and maximal velocity. Excurrent windows in these species tend to be poorly defined by shell features and are lined by quite plastic regions of the mantle. Incurrent windows, in contrast, frequently involve elongated shell siphons. Even in these cases, however, the mantle lining the siphon has overriding control over flow. Lindberg and Ponder (2001) propose that vetigastropods such as *D. aspera* should control the flow through their mantle cavities via the excurrent window whereas caenogastropods such as *F. hunteria* should use incurrent control, but provide no evidence. My observations demonstrate that this is probable and possible because of the Principle of Continuity.

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Form and function of radular teeth of herbivorous molluscs: Focus on the future

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Abstract: The radular apparatus of herbivorous molluscs provides an excellent model for study of form, function, and integration of morphology and function. To date, however, few studies have been conducted in a way that allows us to understand the ecological and evolutionary consequences of different morphologies, and how morphologies differ or are similar in both form and function. I suggest thee areas of focus for future research: (1) Explicit quantification of morphology. (2) Real rather than asserted assessments of function. (3) An integration of structure and function. Taking advantage of new technologies and integrating them with more traditional approaches, experimentation, and quantification of both form and function will prove this to be a rich area for research in the future.

Key words: radula, functional morphology, feeding, herbivore

Although the radula is one of the features characterizing herbivorous molluscs, we know surprisingly little about the ecology and evolution of form and function of this important structure. Hickman (1980) published a very elegant paper directed at paleontologists in which she addressed the evolutionary consequences and considerations of radular tooth form in gastropods and the difficulty of producing a general model of the factors controlling morphology. She categorized these factors as phylogenetic, programmatic, constructional, ecological, maturational, and degenerative (see Hickman 1980: fig. 1). She recognized that not all morphological features of radulae and radular teeth are functionally adaptive or optimized for a specific function and that not all morphology should be viewed in an evolutionary context. Work by Hickman and colleagues (Hickman 1980, 1983, 1984, Morris and Hickman 1981, Hickman and Morris 1985) stressed the importance of understanding how the radular apparatus works, the necessity of examining the radula in its feeding position, and understanding the dynamics of the radula rather than just its static morphology.

Following on work by Littler and Littler (1981), Steneck and Watling (1982) tried to address ecological aspects of the feeding capabilities of herbivorous molluscs. They focused on the feeding capabilities and limitations of herbivores and classified molluscs and seaweeds into "functional groups." For seaweeds, these groups were based on gross morphology and thallus form. In all cases, function (rates of photosynthesis, successional position in a community, grazer resistance) was assumed to correspond in a one-to-one fashion with gross form (see Padilla and Allen 2000, for a recent review of this hypothesis). For molluscs, functional groups were roughly based on taxonomy and overall radular type. Function was inferred from a few studies of diet or best guesses by the authors. For example, they considered all chitons to be functionally the same whether they had radulae with pointed or broad spade-like cusps on their major teeth, if marginal teeth were reduced or long, or if marginal teeth were few or abundant. Similarly, all patellogastropod limpets were assumed to be functionally equivalent, even species with very diverse numbers, shapes, and sizes of teeth.

The hypothesis of Steneck and Watling (1982) was too general and simplistic to adequately address the complexity of functional morphology of the radulae of grazing molluscs. Padilla (1985, 1989) experimentally tested this model for patellogastropods by developing biomechanical techniques to measure the forces required for limpets with different radulae to remove tissue from different algae. The results were opposite to the predictions by Steneck and Watling (1982), and performance differed significantly among patellogastropod species (Padilla 1985, 1989). In addition, she found that cusp shape and number affected the mechanical and functional properties of radular teeth when limpets were feeding on macroalgae.

Given the importance of the radula and its function for grazing molluscs, it is surprising how little progress has been made on the functional morphology of this important and

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diverse structure in the past 20 years. This paper is not intended to be a review of all work that has been done on functional morphology of radulae, but rather to suggest factors that need to be considered and approaches that will facilitate progress in our understanding of the ecology and evolution of form and function of the radulae of grazing molluscs.

There are three areas of research with the greatest potential in the next 20 years: (1) Explicit quantification of morphology. This is not an easy task because the shapes of all complex morphological structures are difficult to quantify in ways that will be meaningful for comparisons among shapes. (2) Real rather than asserted assessments of function. We need to develop methods for testing and demonstrating function, rather than assuming or asserting function on the basis of best guesses. Intuition is limited by past experience and can lead to very wrong conclusions. (3) An integration of structure and function. This includes all of the aspects of structures, their dynamics, and use by organisms.

QUANTITATIVE ASSESSMENT OF MORPHOLOGY

Quantification of Shape

The morphology of complex structures is extremely hard to quantify and has been the focus of the field of morphometrics. Morphometric techniques, especially geometric morphometrics, can be used to quantify morphology in a way that allows morphologies to be described and compared in unambiguous ways. Morphometric methodology has undergone a revolution in the last decade (Rohlf and Marcus 1993, Adams *et al.* in press). Morphometric techniques are used for statistical analyses of variation in shape and are needed whenever shapes are to be compared. They can be used to test whether shapes are similar or different, and in some cases, how they differ. Initially, multivariate statistics were used on a variety of quantitative measures. Geometric morphometrics captures the geometry of structures and preserves this information throughout the analysis. Thus, geometric morphometrics allows statistical analysis of structures with complex shapes and forms, including structures lacking landmarks, which are necessary for more traditional analyses (Adams *et al.* in press).

Collecting Morphological Data

Traditionally, studies have focused on the morphology of hard structures associated with the radula, especially radular teeth. Hard structures usually do not require chemical fixation, and therefore maintain their shape when removed from the animal. Even most descriptions of the shape and morphology of hard structures. however, are qualitative rather than quantitative.

In addition to the focus on hard structures, soft structures should be studied, especially the morphology of structures auxiliary to the radula that are essential for function. Soft body morphology, including the muscles, muscle attachments, the chitinous ribbon, and other structures such as the odontophore must be integrated into our understanding of the morphology of this whole structure. In addition, an understanding of their development will aid in our interpretations of evolutionary changes in form and function (Guralnick and Lindberg 1999).

Tools such as histology can be very helpful, but, can be extremely difficult. Fixation for histology can create artifacts (Voltzow 1990), as can examining dead rather than living animals, and ultimately confuse the interpretation of critical structures.

Microscopy has been a useful tool for studies of morphology. Scanning electron microscopy (SEM) can be a valuable tool for visualizing morphology. However, as with histology, distortions of features of soft tissue can result from fixation and drying of tissues for SEM. The three dimensional form of structures is difficult to assess or quantify from the two dimensional images of SEM. Confocal microscopy is a relatively new tool that is proving to be very useful for visualizing and quantifying some types of structures. Radular teeth that are transparent can be visualized and optical digital sections can be used to reconstruct three-dimensional structures, allowing morphometric analysis of shapes (Padilla, unpublished data).

Mechanical considerations

Biomechanical properties of radular teeth and accessory structures can be extremely important in understanding the relationships between form and function of the radular apparatus. Mechanical properties set the bounds on the potential functional properties of the radula and its components. Morphometrics is a wonderful tool for describing shape independent of size. However, when considering real function and morphology, size matters. The combination of size and shape are important determiners of potential functional performance of radular teeth, especially for their use as tools for feeding.

Mechanical properties of teeth are influenced most by tooth size, the shape of the tooth where it comes in contact with food items, overall shape of the tooth, the materials that teeth are made of, the material properties of the food items, and the interactions among teeth during feeding. The tooth cusp is usually the part of the tooth that comes in contact with food items and therefore is critically important for determining function. The shape of the cusp and the area of the tooth in contact with the substrate affects the amount of force per unit area transferred during feeding. For example, when a limpet is applying its radula to the substrate, a force will be applied at the cusp of each tooth. If the teeth are very pointed, then the total surface area of the tooth in contact with the food item will be less for the total amount of force applied, concentrating the force applied at the tip of each tooth. Thus, pointed teeth concentrate stress and are more effective at piercing and tearing fleshy algae than are blunt teeth (Padilla 1985, 1989). Blunt teeth are broad and have more surface in contact with the substrate when feeding and thus are more effective for rasping and removing loose material from surfaces or broad excavations of brittle materials such as calcified algae. Reductions in the number of teeth per row can also increase the stress experienced at the tip of each of the remaining teeth.

The absolute and relative sizes of the whole tooth are also important, especially the relative size of the length of the tooth to its width. Although long teeth have been proposed to be very effective at excavating algal tissue (Reid 1996), longer teeth should be less stiff and would bend more easily than shorter teeth with the same width. Thinner teeth, for a given length, should also bend more easily. According to beam theory, the ratio of the length to the width dictates how stiff or flexible a tooth (or beam) will be (Wainwright *et al.* 1976, Vincent 1982). Long thin teeth should be flexible and bend when applied to a surface, so are more likely to work in a brush-like fashion. Short, stout teeth should be very stiff and transfer more force to a substrate.

The angle at which a tooth contacts the substrate can also be important. As with machining tools, both cutting angle and clearance angle are important (Padilla 1985). The cutting angle is most important for excavation efficiency. The clearance angle can play an important role in affecting tooth wear with feeding and the potential for changes in tooth shape with use (Hickman 1980). Runham *et al.* (1969) and Vincent (1980) have argued that the structure of patellogastropod teeth enhances their function by increasing wear behind the cusp, which maintains a sharpened edge on the cusp. As a snail feeds and the tooth cusps wear, they work much as a self-sharpening knife, always maintaining their effectiveness. The molluscan radula has even been suggested as a model for improvement of industrial cutting devices (van der Wal *et al.* 2000).

The material properties of teeth are also clearly important. Much work has been done on the mineral properties of patellogastropod radulae and to a certain extent on the radulae of chitons (*e.g.*, Lowenstam 1981). However, surprisingly little work has been done on the material properties or microstructural properties of the radulae of other grazing molluscs.

Morphological variation

The structure of the radula is generally assumed to be constant within a species. However, different radular morphologies have been found within species during ontogeny (Nybakken 1990, Warén 1990, Kawamura *et al.* 2001), among different habitats (Reid and Mak 1999), or when individuals consume different foods (Padilla 1998, 2001). Morphological variability is not expected within all species. For many taxa and for certain aspects of the radula (*e.g.*, numbers of teeth per row of the radula) will be constrained or affected by phylogeny, construction, or use.

Variability within a species may be due to genetic polymorphisms (different genotypes produce alternate morphologies) or phenotypic plasticity (a single genotype can produce different morphologies). Snails in the genus *Lacuna* Turton, 1827 have phenotypically plastic tooth morphologies and individual snails produce different tooth shapes when exposed to different food environments (Padilla 1998, 2001). Although variability has been found in some other species, critical experiments to demonstrate phenotypic plasticity (the ability of individuals to produce alternative phenotypes) have not been performed. If morphologies are phenotypically plastic, it is important to know whether specific morphologies are triggered by certain conditions or whether the shapes of teeth are merely labile within individuals and are not associated with feeding environment or food (Padilla *et al.* 2000, Padilla, pers. obs.).

Interactions among teeth

The dynamics of how teeth move, interact with substrates, and interact with each other are also important for understanding function (Hickman 1984). Studying the dynamics of feeding permits an assessment of how the radula is used as a tool and what aspects of the morphology are important for function. The functionally important aspects of the morphology of the teeth are not always obvious from observations of their static form. Observations of the radula in motion provide a different perspective on which aspects of morphology are important for feeding. For example, frames from videotapes taken of the inside of the mouth *Katharina tunicata* Wood, 1815 show that the teeth work by cutting against one another as well as interacting with the benthic substrate (Fig. 1). Their effectiveness depends upon a scissor-like interaction between teeth, not just the action of individual teeth. At present, it is not known how common this mode of feeding is and how important tooth-tooth interactions are in chitons in general let alone in other molluscs. Presently it does not appear that all chitons show similar feeding patterns (Padilla, pers. obs. Similar videotapes of the patellogastropod, *Lottia scutum* (= *Tectura scutum* Rathke, 1833) "feeding" on a glass surface shows no interactions among teeth (Fig. 2). The radular teeth move together across the substrate, similar to a wood rasp (Padilla 1985).

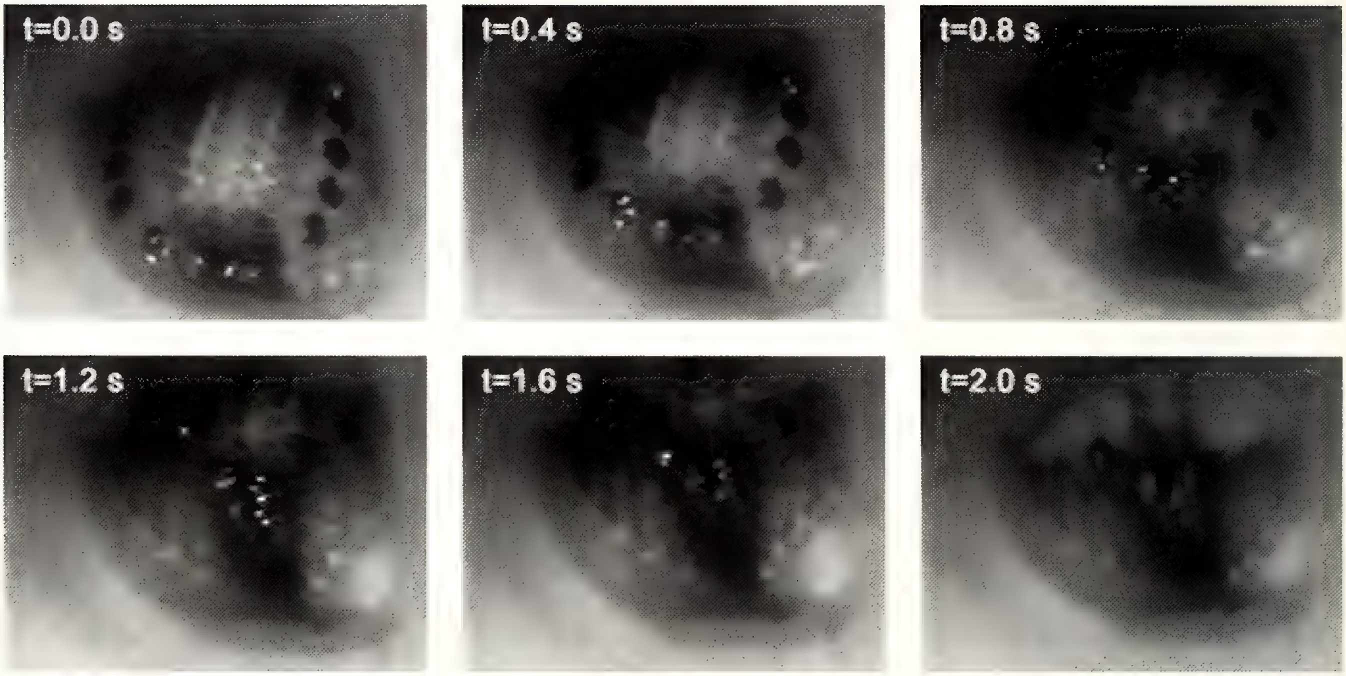

Figure 1. Radular movement of the chiton *Katharina tunicata*. This sequence of the movement of the radula of *K. tunicata* was analyzed by focusing a video camera through the ocular of a dissecting microscope. The chiton was feeding on the side of a glass aquarium. Fiber optic lights were focused on the mouth of the chiton for illumination. The color analog VHS tape was digitally recorded with a video capture system from Pinnacle (DV500). The digital video (avi) file was exported as a image (tif) sequence with Adobe Premiere where it was converted to black and white and the contrast was enhanced. Shown are still black and white frames for every 0.4 seconds during the feeding stroke of the radula.

ASSESSMENT OF FUNCTION

Many scientists have inferred function from morphology. This is risky because nature can be more clever than scientists; intuition can be misleading. To understand the association between morphology and function, we need to observe and quantify function, and then test the role of morphology in affecting function (*e.g.*, Morris and Hickman 1981).

The function of radular teeth has been examined indirectly through impressions that teeth make on substrates when an animal is feeding (*e.g.*, Hickman and Morris 1985). Direct observations of radular movements are still essential, however, to determine how different impressions are made. Initial efforts to visualize feeding required movie film and high light intensity (Morris and Hickman 1981), and proved to be difficult and costly to obtain. Thus, visualizing radular motion has been a technological challenge. Animals are small, usually covered by hard shells, and many of the structures of interest are difficult or impossible to visualize with x-rays or other techniques that are used with larger animals. Computers and low cost digital video systems, including high speed video, permit the direct observation in real time of the movement of the radulae of grazers. For example, videotapes of the radular motion of patellogastropods (Fig. 2) permitted mimicking their mode of use and the measurement of the forces required to remove tissue from different types of algae (Padilla 1985, 1989). Similar approaches with chitons (Fig. 1) indicate the potential scope of functional possibilities.

INTEGRATION OF STRUCTURE AND FUNCTION

Integration of structure and function from all levels of organization is essential (Domenici and Blake 2000). Work on feeding in fishes provides an excellent example of the power of integrating hard and soft morphology, mechanical and material properties and dynamics, and neuromuscular control of feeding (reviewed in Wainwright *et al.* 2000). Most fishes are much larger than herbivorous molluscs and their combination of a soft tissue exterior with a calcified internal skeleton greatly facilitates visualization. Similar types of integration will be more difficult with small, soft-bodied molluscs. Molluscs have been used as models to study the neural control of muscular systems, and much work has already been done on the neuromuscular control of radular movements in gastropods (Elliott and Susswein 2002), especially in terrestrial and sea slugs. However, unlike fishes, there have been no attempts to integrate physiological mechanisms with radular function and morphology.

The radular apparatus of herbivours molluscs provides an excellent model for study of form, function, and integration of morphology and function. Integration of new technologies with more traditional approaches, coupled with experimentation and quantification of both form and function will prove to be a rich area for research in the future.

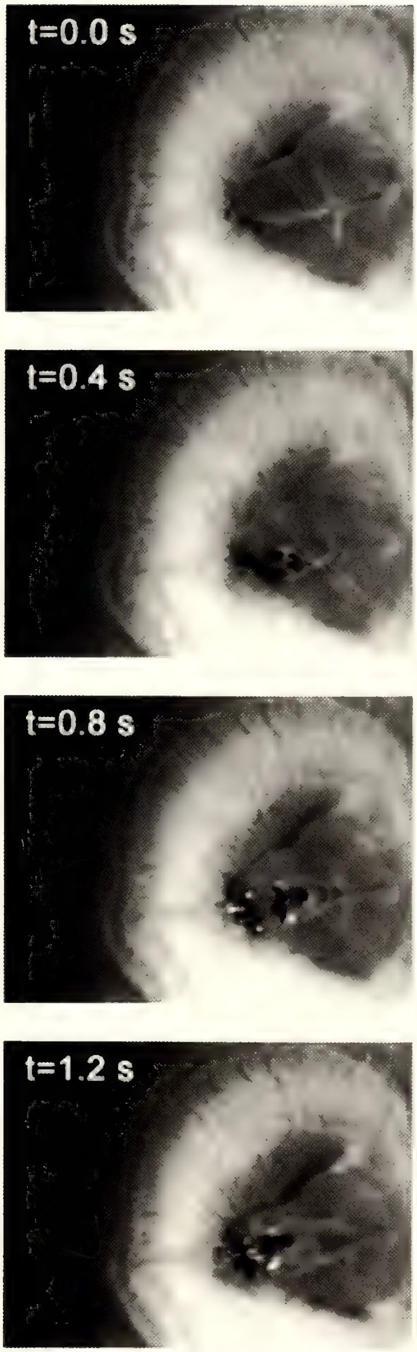

Figure 2. Radular movement of the docoglossan limpet, *Lottia scutum*. This sequence of the movement of the radula of *L. scutum* was analyzed by focusing a video camera through the ocular of a dissecting microscope. The limpet was feeding on a glass slide inverted in a dish of sea water. Fiber optic lights were focused on the mouth of the limpet for illumination. The color analog VHS tape was digitally recorded with a video capture system from Pinnacle (DV500). The digital video (avi) file was exported as a image (tif) sequence with Adobe Premiere where it was converted to black and white and the contrast was enhanced. Shown are still black and white frames for every 0.4 seconds during the feeding stroke of the radula.

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70th Annual Meeting

American Malacological Society

Sanibel Island, Florida
31 July–4 August 2004

Fellow Malacologists,

I am glad to announce that the 70th Annual Meeting of the American Malacological Society will take place on beautiful Sanibel Island, Florida, from Saturday, July 31, to Wednesday, August 4, 2004. Sanibel Island is a world-renowned, nature-oriented travel destination that is also famous for its bountiful molluscan resources. The event will be hosted by The Bailey-Matthews Shell Museum and will have as its main venue the Sundial Beach Resort, located on the eastern part of the island.

The American Malacological Society is a dynamic international society of individuals and organizations with an active interest in the study and conservation of molluscs. AMS covers a wide range of subjects in the field of molluscan studies, and its meetings, symposia, sessions, posters, and special events reflect that.

A symposium on the Relationships of the Neogastropoda will be convened by M. G. Harasewych of the National Museum of Natural History at the Smithsonian Institution. Special sessions will include Biodiversity of Marine Mollusks (organized by Gustav Paulay, Florida Museum of Natural History); Coastal Molluscan Assemblages as Environmental Indicators (Michael Savarese, Aswany Volety, and Greg Tolley, Florida Gulf Coast University); Systematics of Freshwater Gastropods (Russel Minton, University of Louisiana at Monroe); Terrestrial Mollusks as Agricultural and Environmental Pests (David Robinson, United States Department of Agriculture/Academy of Natural Sciences of Philadelphia), and Global Marine Bivalve Database Workshop (Gustav Paulay, Florida Museum of Natural History, Paul V. Scott, Santa Barbara Museum of Natural History and Graham Oliver, National Museums & Galleries of Wales). In addition, a special forum organized by Ken Hayes, Anna Bass, and Amy Wethington, all graduate students in malacology, will focus on and discuss common issues and problems faced by soon-to-be professionals in the field.

The 70th Annual Meeting will be sponsored by the American Malacological Society, The Bailey-Matthews Shell Museum, and the Sanibel-Captiva Shell Club, with additional support from the Sanibel-Captiva Chamber of Commerce, Sundial Beach Resort, J. N. "Ding" Darling National Wildlife Refuge, Florida Gulf Coast University, and Captiva Cruises.

The Sanibel-Captiva Shell Club will sponsor the Shell Museum Open House on Sunday, August 1. The closing banquet will be a dinner-cruise aboard Captiva Cruises's *Lady Chadwick*, a two-deck vessel holding 250 passengers. Specially priced rates at the Sundial Beach Resort will be available for meeting participants at $110/night for regular rooms, $125 for the Gulf View rooms, and $175 for two-bedroom suites. Sundial is willing to accommodate up to 6 students per suite, which will lower the cost of accommodations for these low-budget participants.

Three field trips are planned for the last day of the meeting, Wednesday, August 4: A nature-watching visit to J. N. "Ding" Darling National Wildlife Refuge on Sanibel, guided by professional ornithologist and Shell Museum volunteer Dr. Jon Greenlaw; a daylong boat trip to Cayo Costa State Park guided by senior Shell Museum staff (located on isolated and undeveloped Cayo Costa, the park offers pristine views of the Gulf, dunes, lagoons, and opportunities for shell collecting; no live-mollusc collecting is allowed in the park or elsewhere in Lee County); and a visit to a Plio-Pleistocene fossil pit in Sarasota County guided by Roger Portell, invertebrate paleontologist at the Florida Museum of Natural History.

More than 24 airlines service Southwest Florida International Airport in neighboring Fort Myers (30 minutes from Sanibel). The Lee Island Coast region and surrounding areas offer many opportunities for side trips on your own, depending on your interest: Edison-Ford Winter Estates, Miracles baseball games, and Everglades National Park, to name a few.

More information about the meeting will be provided on the AMS and Shell Museum Web sites as it becomes available.

Cordially,

José H. Leal, PhD
President, American Malacological Society

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